

CHAPTER 7

LATERALIZED BEHAVIORS IN THE GLOSSY BLACK-COCKATOO, AND THE EVOLUTION OF LATERALITY

ABSTRACT

Parrots are reputed to use the left foot for holding food, and are often cited as the best example of species-level behavioral laterality comparable to human handedness. The existing data, however, are not adequate to unequivocally demonstrate consistent “footedness” at the population level for any parrot species. It is also unclear what kinds of behaviors tend to be lateralized, and whether foot preferences are learned in captivity. I examined six asymmetric behaviors in an Australian parrot, the glossy black-cockatoo (*Calyptorhynchus lathami*) in the wild. Only behaviors involving manipulation of food items were strongly lateralized at the population level. These included use of the foot, as well as the bill and tongue. This is the first demonstration of a population-level side preference involving a central rather than a paired appendage. This type of laterality is not consistent with existing explanations for behavioral laterality, which are based on brain asymmetry. I propose an alternative hypothesis for the function of behavioral laterality based on improved learning of complex motor skills. I also explore the implications of this hypothesis for other vertebrate taxa, where it may have broader explanatory power than hypotheses based on structural brain asymmetries.

INTRODUCTION

Lateralized behaviors are asymmetric and can be performed on either side of the body, but are directed to one side disproportionately often. Individual animals often show consistent preferences performing particular behaviors on one side (individual-level laterality), but it is rare for such “sidedness” to be consistent in direction across a population or species (population-level laterality). Population-level laterality initially attracted attention because it was thought to be a uniquely human trait (Warren 1980, Corbalis 1988). This is apparently not true, but the extent of weaker population-level laterality in non-human primates is still an area of active research (e.g., Bradshaw & Rogers 1993, Ward & Hopkins 1993). However, many recent authors regard parrots as proof that population-level laterality is not unique to either humans or primates. Most parrot species hold and manipulate food items with the foot, and parrots are generally regarded as showing population-level laterality comparable to that of humans in their foot preferences. Harris (1989) reviewed the literature on parrot “footedness” and found that most workers cite just two studies (Friedmann & Davis 1938, and Rogers 1980). Four other studies have reported data on food holding preferences (McNeil et al. 1971, Smith 1972, Cannon 1983, Nos & Camerino 1984 in Harris 1989). Of the 34 species studied altogether, 23 held food more often in the left foot, nine in the right foot, and two showed no difference. Four of these species also preferred the same foot for removing sticky tape from the bill (Gunturkun et al. 1988). Although no quantitative studies have been conducted, field observations indicate that glossy black-cockatoos are highly lateralized for food holding (reviewed in Magrath 1994).

Given the number of studies conducted and the wide acceptance of the idea in the literature, it is surprising that no study has unequivocally demonstrated population-level

laterality in any parrot species. Many studies either included too few individuals to reveal population-level biases, or did not identify individuals at all. Others pooled data across individuals, making them inappropriate for testing population-level effects (Machlis et al. 1985). Data on enough individuals to test statistically for a population-level bias have been reported for only two species: brown-throated parakeets holding food (*Aratinga pertinax*; McNeil et al. 1971), and budgerigars removing tape from the bill (*Melopsittacus undulatus*; Rogers & Workman 1993). There was no evidence for population-level laterality in either. Nonetheless, recent writings continue to cite parrots as exhibiting population-level behavioral laterality (e.g., Corballis 1987, Iacino 1993, Rogers & Workman 1993).

A second factual question regarding parrot footedness is whether individual parrots learn their foot preferences by interacting with right handed humans (Smith 1972, Harris 1989). In support of this suggestion, several species do alter their foot preferences if consistently offered food from one side (Smith 1972, Cannon 1983). No captive studies have attempted to control for the effects of human interactions. Several species have been observed in the wild, but in each case the sample size of individuals was unknown (Rogers 1980, Cannon 1983, Prendergast 1985, Magrath 1994).

There are also questions about how parrot foot preferences should be interpreted. Most authors assume that parrots favor one foot for holding and manipulating food items. However, because a parrot holding food is also perching on one foot, a preference for the perching foot is an equally plausible explanation (MacNeilage et al. 1987 p. 296, Harris 1989). If parrots do have a perching-foot preference, they should show it when the other foot is resting rather than holding food, but no data are available on this point. The question of whether parrots prefer one foot for perching (a strength task) or handling food (a dexterity task) is relevant to a current debate about laterality in birds. Limb preferences are associated with the manipulation of objects in many species (Walker

1980), and several authors have suggested that this is true of parrots as well (Gunturkun et al. 1988, Harris 1989). However, other workers have argued that behavioral laterality in birds is associated with visually guided behaviors rather than object manipulation (Davies & Green 1991, Rogers & Workman 1993).

Behavioral laterality has been studied mainly in primates. The field is marked by controversies over experimental design, statistical methods, and interpretations of results. Population-level laterality is undisputed in humans, with hand use usually estimated at about 90% right-biased (Annett 1985). There is evidence for weaker population-level hand preferences in other primates, but this is still hotly disputed (e.g., MacNeilage et al. 1987, Bradshaw and Rogers 1993). The only other mammals with known laterality at the population level are cetaceans. Most humpback whales prefer the right flipper for slapping the water (*Megaptera novaeangliae*; Clapham et al. 1995), and there is evidence of behavioral laterality in grey whales (*Eschrichtius robustus*; Kasuya & Rice 1970) and bottlenose dolphins (*Tursiops truncatus*; Hoese 1971). In birds other than parrots, there is a single report of population-level laterality in chickens scratching the ground with a foot (Rogers & Workman 1993).

If population-level behavioral laterality is characteristic of primates, cetaceans and parrots, these taxa are phylogenetically isolated enough that it probably evolved independently in each. Whether this represents convergent evolution is not clear, however, because we know so little about the functions of behavioral laterality. Formulating and testing the broadest possible explanations for the origin and function of population-level behavioral laterality will require comparative studies on a wider array of species.

The present study examines behavioral laterality in an Australian parrot, the glossy black-cockatoo (*Calyptorhynchus lathami*), in the wild. This species feeds almost exclusively on small seeds extracted from the woody cones of casuarina trees

(*Allocasuarina* spp.) (Forshaw 1978). The population I studied feeds on drooping sheoak (*Allocasuarina verticillata*) seed cones, which on average weigh 5.8 g and contain 96 tiny seeds weighing 3.6 mg each (Chapter 4). They reportedly hold seed cones in the left foot in the field (Magrath 1994), and shift the lower bill to the left while husking seeds in aviaries (Sindel & Lynn 1989). To clarify the existence, nature, and implications of behavioral laterality in this species, I collected laterality data on these feeding behaviors as well as some non-manipulative behaviors.

METHODS

Three field assistants and I observed a habituated flock of glossy black-cockatoos during Sept. - Nov. 1991 and Jan. - Aug. 1993 at Stokes Bay, on Kangaroo Island, South Australia. We recognized individuals using distinctive plumage markings and other features (Chapter 1). The study flock included 27 known individuals, including 13 adult females and 14 adult males, as well as several males in sub-adult plumage that were not individually recognizable. All observations were of cockatoos perched in trees.

The foot used to hold drooping sheoak (*Allocasuarina verticillata*) seed cones was recorded during a study of foraging ecology (Chapter 4). The cockatoos often handled many seed cones in sequence without changing position. To ensure independence of data points, I therefore scored feeding bouts rather than individual seed cones. Each bout consisted of one individual in one tree during a 30 minute interval, and included an average of 11.2 seed cones. I scored bouts as right or left footed based on which foot was used to hold the majority of cones handled.

I recorded the sidedness of five other behaviors *ad libitum* during both the foraging study and a study of social behavior (Chapters 5 & 6). These included: perching

on one foot while resting; holding one wing away from the body (on hot days, apparently for thermoregulation); turning the head back over one shoulder while sleeping; and closing the tail such that one of the outermost tail feathers crosses in front of the other. The final behavior, bill shifting, occurred while the cockatoos ate. After gouging a mouthful of material from a seed cone they lowered the cone and worked the material inside their bill, apparently separating the seeds from chaff and husking them. During this process they briefly shifted the lower mandible to one side. They sometimes pushed pieces of shredded cone out of the bill, always on the same side the lower mandible was shifted toward. To ensure the independence of *ad libitum* data points, I only scored the same individual performing the same behavior twice on the same side if at least 10 minutes passed between observations, and the relevant behavior was completely interrupted. I did not apply these restrictions if the behavior was repeated on the opposite side.

To test for a population-level bias in a given behavior I determined which side each individual used most often, then used a two-tailed binomial test for deviation from a 1:1 ratio of right and left-biased individuals. To test for individual-level bias I used a two-tailed binomial test on all observations of one individual performing one behavior.

RESULTS

The cockatoos showed population-level lateral biases at the 100% level for holding seed cones and for shifting the lower bill while sorting seeds (Table 7.1). No cockatoo ever shifted its bill to the left, and only one held a seed cone in the right foot. (This subadult female ate one entire seed cone while holding it in her right foot.) Pooling all bouts, the cockatoos held all but one of 1382 cones in the left foot. The cockatoos showed weaker (87-89%) biases for perching on one foot and holding one wing open,

which were also significant at the population level. Sleeping position was not lateralized at either the population or the individual level; there were large enough samples for one-tailed statistical tests on six individuals (N ranged from 5 to 11), none of whom showed a significant bias ($p > 0.14$ for each). We observed tail folding too few times for statistical analysis.

Table 7.1. Summary of data on lateralized behaviors. The values under “Pooled observations” combine observations on all individuals to indicate population averages. Values under “Number of individuals” indicate how many individuals performed the behavior more often on each side. P values are for two-tailed binomial tests for population-level bias.

<u>Behavior</u>	<u>Pooled observations</u>		<u>Number of individuals</u>		
	<u>N</u>	<u>% Left</u>	<u>Left biased</u>	<u>Right biased</u>	<u>p value</u>
Hold seed cone in foot	128	100.0%	17	0	.000
Shift lower bill	35	100.0%	14	0	.000
Raise foot while resting	23	13.0%	10	0	.002
Hold one wing open	18	11.1%	1	6	.218
Turn head back to sleep	78	57.7%	11	7	.548
Fold tail feather in front	5	40.0%	1	1	

DISCUSSION

Lateralized behaviors in glossy black-cockatoos

This study provides unequivocal evidence for population-level behavioral laterality in a parrot. All individuals were completely lateralized for food holding. The single observation of right-footed cone holding represented 0.07% of the total observations, but the actual degree of laterality in this population may be even greater than this figure suggests. I did not see any other cases of food holding with the right foot during two years of field study, and Joseph (1989) also noted exclusive use of the left foot by glossy black-cockatoos on Kangaroo Island in 45 hours of observation. Thus this is among the most highly lateralized behaviors described in any animal. The bias is not attributable to any known asymmetry in *Allocasuarina* seed cones, which are radially symmetrical without a clockwise or counterclockwise spiral (Wilson & Johnson 1989, J. Pepper, pers. obs.). This laterality is probably not learned, as it appears to be a nearly universal characteristic of the species (Hyem 1933, Readers Digest 1976, Thatcher 1988, Joseph 1989, Sindel & Lynn 1989). Magrath (1994) observed a right-footed male on two occasions (probably the same individual), but recounts many other field observations of left-footed feeding.

The cockatoos were also 100% lateralized in shifting the bill while handling seeds. Bill laterality did not appear to be attributable to biased foot use, because the foot and seed cone were not in contact with the bill while it was shifted to the side. The species also lacks any known anatomical asymmetry of the bill or tongue. Movements inside the bill were not visible, but according to Forshaw (1978), a feeding parrot typically “uses its thick tongue to steady the seed against the broad, ridged underside of

its upper mandible and with the front cutting-edge of the lower mandible peels away the seed-coat” (p. 29). Although they eat smaller seeds than most parrots, glossy black-cockatoos do apparently husk each seed individually (Sindel & Lynn 1989, p. 127). Bill-shifting appears to be involved in either separating seeds from shredded cone material, or splitting them to remove the kernel.

To my knowledge this is the first demonstration of a population-level side preference involving a central rather than a paired appendage. Two lemur species have side preferences for using the molars in feeding, but laterality is consistent only at the individual and not the population level (Stafford et al. 1993, Bennett et al. 1995). Moreover, the hands are also involved in the lateralized feeding behaviors, and individuals show strong individual preferences for hand use. Thus mouth laterality is not independent of hand laterality, and may be a secondary effect. Laterality research has been largely confined to primates, and behaviors involving medial appendages in other species may have been overlooked. Possible candidates include elephants or primates using trunks or tails to grasp and manipulate, cetaceans using the tail or rostrum, and any animal that learns specialized food-handling techniques using only the mouth parts.

Although the cockatoos showed a statistically significant bias for lifting the right foot while resting and a trend toward holding the right wing open, both were probably secondary effects of the food holding preference. Most observations were of feeding birds, and it is probably easier for them to open the right rather than the left wing while the left foot is raised to feed. Similarly, the perching foot preference was not consistent across contexts, as they usually perched on the left foot while resting but the right while feeding. The resting preference probably arose simply because they took advantage of infrequent opportunities to rest the perching muscles in their right foot. They spend most of their daylight hours feeding, and thus perching on the right foot (Chapter 5).

The other two postural behaviors showed no evidence of laterality. Sleeping position was not lateralized at the individual or population level. Too few observations were available on tail folding for a statistical test, but it appears to be much less lateralized than food holding or seed sorting.

What kind of behaviors are lateralized?

No evidence was previously available on whether footedness in parrots reflects a preference for the foot used to perch, or for the foot used to hold and manipulate food. Smith claimed that black-headed caiques (*Pionites melanocephala*) show a consistent perching-foot preference whether feeding or not (1971), then retracted this statement (1972), but did not report his methods or data. No other studies have addressed this point. The fact that glossy black-cockatoos did not show a consistent perching-foot preference across contexts shows that they prefer one foot for holding seed cones, rather than for perching.

This finding, as well as the other results, are consistent with the idea that only behaviors involving object manipulation are highly lateralized in parrots. Holding cones is not a simple grasping behavior. Instead, the foot constantly manipulates and re-orientes the seed cone (Chapter 3). Separating tiny seeds from shredded cone material, and splitting them and removing their contents, also presumably entails complex manipulations. The weaker lateral biases in non-manipulative behaviors were probably secondary effects. Comparisons across parrot species also suggest that population-level laterality is associated with object manipulation. Parrots are exceptional among birds in their “manual” dexterity, and also have unusually complex jaw and tongue musculature (Brooke & Birkhead 1991, p. 105). There is evidence against population-level footedness in only two parrots, the budgerigar (Rogers & Workman 1993), and the brown-throated parakeet (McNeil et al. 1971), and both are exceptions to the rule that parrots manipulate

objects with their feet (Forshaw 1978). In contrast, the current results are not consistent with the hypothesis that avian laterality arises in visually guided behaviors (Davies and Green 1991, Rogers and Workman 1993). Seed husking occurs entirely inside the bill, and therefore does not involve vision, yet it was extremely lateralized.

The fact that laterality is associated with object manipulation in both primates and parrots is consistent with the idea of convergent evolution in the two orders. It may also be significant that across species, strong population-level laterality is associated with specialized diets, and stereotyped behaviors for handling particular food items, both in parrots (Cannon 1983, Joseph 1989), and in primates (Stafford et al. 1993, Bennett et al. 1995).

What is the adaptive significance of lateral behaviors using medial appendages?

All previous hypotheses for the adaptive significance of highly lateralized behaviors are based on functional asymmetry in the brain. In many vertebrates the two brain hemispheres are differentiated both structurally and functionally, so that each hemisphere is “dominant” for certain mental processes, which it conducts more effectively, or to a greater extent, than the other hemisphere (Denenberg 1981). Although best documented in mammals, hemispheric dominance has also been shown for singing in male songbirds (Nottebohm 1977).

In vertebrates, each hemisphere has direct sensory and motor pathways to only one (opposite) side of the body. This, together with the fact that both hemispheric dominance and behavioral laterality were thought to be uniquely human, led to the idea that behavioral laterality is caused by brain asymmetry. According to this view, tasks such as object manipulation use cognitive processes that one hemisphere is dominant for, and therefore they can be performed best by the limb that is directly controlled by the dominant hemisphere. In some scenarios the dominant hemisphere became specialized as

a direct result of natural selection for proficiency in a specific skill (e.g., tool use, throwing or feeding; see MacNeilage et al. 1987 for review). In other versions one hemisphere became dominant by default when the other became specialized for a different process (e.g., emotion and attention; Denenberg 1981). In all these scenarios, however, behavioral laterality is advantageous because it brings to bear the more competent rather than the less competent brain hemisphere. This assumption has remained an underpinning of most ideas about the evolutionary origins and functions of behavioral laterality.

The hypothesis that lateralized behavior arises as an incidental effect of lateralized brain structure works well for paired appendages, which have direct neural connections to only one hemisphere, but it does not apply to medial appendages such as bills and tongues. These centrally located organs are supplied with paired motor and sensory nerves, with the members of each pair connected to opposite brain hemispheres. Furthermore, because fine motor control depends on antagonistically paired muscles, precise lateral movement of medial appendages must involve both hemispheres. Thus hemispheric specialization can explain lateralized behavior only in paired, and not medial, appendages.

The learning advantage hypothesis

Is there a functional explanation for strongly lateralized behaviors involving medial appendages? One possible explanation lies in the learning advantage provided by behavioral laterality. An asymmetric behavior performed on two different sides constitutes two distinct behaviors, in the sense that each involves a different set of sensory inputs and motor outputs. This means that skills learned through practice on one side do not transfer to the other side. (You can easily demonstrate this to yourself by reversing the roles of your two hands while tying your shoelaces.) By specializing on one

side, a completely lateralized individual can effectively practice one behavior instead of two. By doubling the frequency of practice, any given level of proficiency can be reached in half the time it would take a non-lateralized individual. This “learning advantage” hypothesis differs from the hemispheric dominance hypothesis in that the benefit of laterality does not lie in using one particular side over the other, but rather in using *either* side preferentially. Also unlike the hemispheric dominance hypothesis, it does not require any asymmetry in brain structure or function beyond that required to bias the behavior to one side.

Learning does appear to be important in glossy black-cockatoo feeding behavior in the wild. Food handling skills develop slowly (Clout 1989, Chapter 3), and techniques vary geographically (Joseph 1983), suggesting that food handling skills are learned. Adults handle seeds very rapidly, taking only about two seconds per seed to extract them from the cone, separate them from shredded cone material, split them open, and remove the kernel (Chapter 4). Moreover, food handling time appears to be a limiting factor in the species energy budget (Clout 1989, Chapter 4). Thus the speed with which they can perform these behaviors may be under strong natural selection. Parrots in general are well known for their ability to learn complex motor skills (e.g., Moore 1992), and there is evidence that other members of the black-cockatoo genus also learn food handling skills in the wild (McInnes & Carne 1978, Saunders 1979).

The learning advantage hypothesis may apply to animals other than parrots, and may be more broadly applicable than the hemispheric dominance hypothesis. Unlike the hemispheric dominance hypothesis, it applies to both medial and paired appendages, and can also explain behavioral laterality that is restricted to the individual level. Such cases are far more common than examples of population-level laterality, both in primates (Fagot & Vauclair 1991) and in other mammals (Walker 1980). In contrast, the asymmetries in brain structure associated with hemispheric dominance are consistent only

at the population level (Denenberg 1981). Thus the hemispheric dominance hypothesis cannot explain most known cases of behavioral laterality. In contrast, under the learning advantage hypothesis the side used must be consistent within an individual to provide a fitness benefit, but need not be consistent between individuals. According to this hypothesis, complex object manipulations are lateralized because they require learning through practice, not because they require cognitive processes that are concentrated in one hemisphere. Thus the learning advantage hypothesis offers a more general explanation of behavioral laterality than the hemispheric dominance hypothesis.

Neither the learning advantage hypothesis nor the hemispheric dominance hypothesis explains the phenomenon of consistent laterality at the population level. We do not understand the functional significance of this pattern any better for structural than we do for behavioral asymmetries (Bradshaw 1981). The existence of anatomical asymmetries is crucial, but their direction is not - a mirror image human with the heart on the right side would presumably work just as well. Nonetheless, most anatomical asymmetries are consistent at the population level in vertebrates. One possible explanation is that mechanisms that produce population-level laterality are more developmentally stable and reliable, giving them a fitness advantage over mechanisms that produce only individual-level laterality. There is some support for this idea in regard to behavior. Compared to population level biases, those appearing only at the individual level are often relatively weak, and completely lacking in some individuals (for reviews see Walker 1980, Denenberg 1981).

Testing hypotheses for the functional significance of behavioral laterality

The hemispheric dominance and learning advantage hypotheses are not mutually exclusive. In fact, if a learning advantage causes population-level laterality to arise and persist, one might expect brain asymmetries to evolve as a result. For any given case,

however, the two hypotheses can be tested separately, because each leads to some unique predictions. Only the hemispheric dominance hypothesis predicts that lateralized behaviors will always co-occur with hemispheric dominance for a cognitive skill that is critical to the behavior, and that the behavior will involve the side of the body opposite the dominant hemisphere. Only the learning advantage hypothesis predicts that the lateralized behaviors will require substantial learning through practice to reach proficiency.

I have already discussed two categories that do not seem to fit the hemispheric dominance hypothesis: lateralized behavior of medial appendages, and behaviors that are lateralized only within individuals and not populations. Another possible category is population-level behavioral laterality that varies between related species. Asymmetries in brain structure are not evolutionarily labile, probably because their underpinnings are genetically and developmentally complex. Thus directional differences in brain asymmetry do not occur between lower taxonomic units such as genera within a family (Dennenberg 1981). In contrast, population-level behavioral laterality is apparently more variable, at least in parrots. This parrot order is monophyletic (Forshaw 1978), and although most species are reportedly left footed, several species appear to be consistently right footed. These fall into two groups, the tribe Arini (Nos & Camerino 1984, Smith 1975 for systematics) and the rosellas (*Platycercus spp.*; Rogers 1980, Cannon 1983, Gunturkun et al. 1988). It seems unlikely that hemispheric dominance is reversed from the usual pattern in these two groups, as the hemispheric dominance hypothesis would predict, but this can be determined by neuroanatomical studies.

The learning advantage hypothesis leads to several predictions for any lateralized behavior. One is that performance should be better on the preferred side, and another is that more highly lateralized individuals should show higher proficiency. In contrast, the hemispheric dominance hypothesis makes similar predictions only in cases of population-

level laterality. A failure to find these patterns in behaviors lateralized only at the individual level would therefore falsify the learning advantage hypothesis. Cotton-top tamarins have hand preferences in reaching for food at the individual level only, and right- and left-handed individuals perform equally well. However, within individuals the preferred hand was more accurate than the non-preferred hand (King 1995). Similar results were reported for capuchin monkeys (Fragaszy & Mitchell 1990), and baboons (Trevarthen 1978). Moreover, stronger behavioral laterality in reaching and grasping was correlated with higher performance in tamarins (King 1995), as well as squirrel monkeys (data from King & Landau 1993, re-analyzed by King 1995). These results are consistent with the learning advantage hypothesis, but do not bear on the hemispheric dominance hypothesis because it is not applicable to these behaviors.

The learning advantage hypothesis specifically predicts that behavioral laterality be associated with learning. In this regard, it may be significant that the three orders in which behavioral laterality is best established, primates, cetaceans, and parrots, are also those with the largest proportional brain size among mammals and birds respectively (Pearson 1972, Jerison 1973).

Any behavior that was strongly lateralized, but not learned through practice, would be incompatible with the learning advantage hypothesis. I am not aware of any such cases in vertebrates. Field crickets show population level laterality in rubbing the wings together to produce song, apparently without any anatomical basis (Alexander 1961, p. 192). This behavior may also require practice to perfect, because crickets artificially made to change sides required several days to achieve normal adult song, as they do when first molting to adulthood (Rakshpal 1960). Population-level laterality in learned object manipulations might also be predicted under the hemispheric dominance hypothesis, if it involved a lateralized cognitive function. Therefore the best independent tests of the learning advantage hypothesis might involve behaviors lateralized at the

individual level only. Only under the learning advantage hypothesis is there reason to expect that all such behaviors should be learned.

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