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Short Communications

Absence of Footedness in Domestic Pigeons

Handedness is the most obvious aspect of the lateralization of the human brain, and most studies on cerebral asymmetries in humans have been concerned with this topic. As a consequence, many experiments dealing with potential functional lateralizations in animals deal with the putative analogue to human handedness, namely forelimb preferences (Denenberg 1981). These studies indicate that limb-use preferences occur particularly in those mammals that use their forelimbs not only for standing or locomotion but also for fine manipulations (for a comprehensive review see Walker 1980). If this were to extend to birds, one would predict that those birds that use their hindlimbs for complicated manipulations of food items or nest material should show 'footedness', while those birds that perform such fine handling only with their beaks should not.

Parrots are well known for their skill in grasping and holding food items with one foot while feeding. Two studies have indeed revealed that several of the South American and Australian parrots (Psittacidae) have marked foot preferences. Apart from two right-footed species, 14 parrot species examined had a significant sinistral bias (Friedman & Davies 1938; Rogers 1980). During experiments in which hungry goldfinches, *Carduelis carduelis*, had to clear 12 different doors with various catches and bolts on their way to a feeding compartment, Dücker et al. (1986) observed that they exclusively used their right foot besides the beak to open the obstacles. Under natural conditions goldfinches are known to use their feet to hold thistle inflorescences when extracting the seeds with the beak. Various other species of birds are also reported to perform complex manipulations with their feet and some behavioural patterns like 'string pulling' have been closely analysed under experimental conditions (Vince 1961). As far as we know, however, in none of these studies were foot preferences analysed separately. Since most birds do not use their hindlimbs for any complex food handling it is difficult to devise suitable tests of footedness for them. However, all birds use a single foot at a time for at least one behaviour and that is for head scratching. Therefore we examined whether pigeons, which do not use their limbs for fine manipulations, do demonstrate footedness in this context.

The subjects were 50 adult domestic pigeons, *Columba livia*, of homing stock and undetermined sex. During the experiment, the birds were kept in individual wire mesh cages, separated by blinds. To elicit beak scratching a small ($1{\cdot}5 \times 1{\cdot}5$ cm) piece of sticky tape was affixed to the upper tip of the beak. Great care was taken to place the tape medially, without any lateral bias. Then we observed from a distance of about 3 m with which foot the animal attempted to remove the tape. After the first such attempt was scored the tape was immediately removed to prevent habituation. Each pigeon was tested once a day on 5 consecutive days.

Mostly the animals immediately tried removing the tape by vigorous head shaking followed by scratching. During the 250 observations the pigeons used the left foot 133 times and the right foot 117 times ($P > 0{\cdot}1$, binomial test). While this observation indicates no left–right bias at the population level, it is still possible that there are nearly equal numbers of left-footed and right-footed birds. Figure 1 presents the frequency of birds classified according to the foot-use shown during the five tests. It is evident from the symmetric unimodal distribution that there is no lateral bias. Even the two animals that used their left foot five times can hardly be interpreted as indicative of a small subpopulation with sinistral bias. According to a binomial distribution 1·56 animals would be expected to behave so by chance, in the absence of any consistent side preference.

The results suggest that there is no footedness in pigeons, at least with respect to the task of removing a sticky object from the tip of the beak and where either leg could be conveniently used. It is not certain though that the task is a valid test for footedness. If so, parrots should prefer the same hindlimb for beak scratching as they use for manipulating food. If they have such a preference, it could be argued that pigeons have no foot preference.

To test this, several parrot species previously shown to display footedness during food manipulations (Friedman & Davies 1938; Rogers 1980) were examined for limb preferences during tape removal. Since initial attempts with untamed zoo animals turned out to be dangerous, tame circus parrots were sought. Six individuals belonging to four different species were available: *Cacatua gallerita*, *Ara macao* (two animals of each species), *Ara severa*, *Platycercus elegans* (one individual of each species). All of these species are left-footed for food handling except *Platycercus elegans* which is right-footed (Friedman & Davies 1938; Rogers 1980). To elicit beak scratching a piece of sticky tape ($5 \times 1{\cdot}5$ cm) was affixed along the midline of the beak. The foot with which the animals tried to remove the

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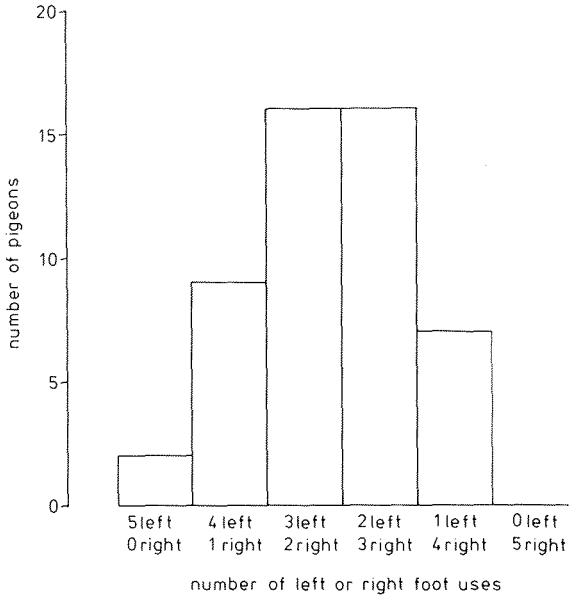

Figure 1. Number of left and right foot uses during the five tests performed with each of 50 pigeons.

tape was recorded. All the parrots used the hindlimb known to be dominant for food grasping ($P < 0{\cdot}05$, binomial test). This result demonstrates that in parrots the limb that is dominant for food handling is also preferentially used for beak scratching.

A third experiment was conducted with humans, the only mammalian species known to have a limb preference at the population level. The experimental subjects were 30 randomly selected students (15 males, 15 females). To prevent biases the persons were not informed that they participated in a handedness study but were instead asked to take part in a time estimation experiment. Subjects were tested singly. To begin with, each subject was asked to estimate the elapsing of 10 s after the experimenter had started a stopwatch. Then they were told that the same procedure was now to be repeated under modified sensory conditions. A small piece of sticky tape ($1{\cdot}5 \times 1{\cdot}5$ cm) was stuck on their nosetip. After the subjects had again estimated the duration of 10 s, they were told that they could remove the tape. The hand which they used was recorded. They were then asked whether they were primarily left-handed or right-handed and were informed about the true purpose of the experiment. Twenty-eight students said that they were right-handed. Out of the 30 students 24 used the dominant hand to remove the tape ($P < 0{\cdot}01$, binomial test). Thus both parrots and humans appear to use preferentially the dominant limb for grooming the body midline.

The results suggest that there is a causal link between handedness or footedness and limb preference during head scratching. The absence of a foot preference in pigeons during tape removal can thus be taken to indicate a general lack of footedness in this species. This does not imply a general absence of lateralization in pigeons, since, for example, it is well established that their visual system is strongly lateralized (Güntürkün 1985). Our results support the hypothesis that limb use preferences in general occur only in species that use their limbs for manipulative activities (Walker 1980). If true this would indicate that a selection pressure arises for the assembly of special lateralized neuronal structures whenever there is need for fine handling with limbs. A lateralization of motor structures controlling hindlimbs would then be absent in species that, like pigeons, use their beak for the manipulation of objects. On the other hand one would expect asymmetries in the neuronal control of fine manipulative motions with the beak. Future research will show whether unilateral lesions of the nucleus basalis, a key structure for the control of pecking in pigeons (Delius 1985; Schall et al. 1986), has asymmetric effects.

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