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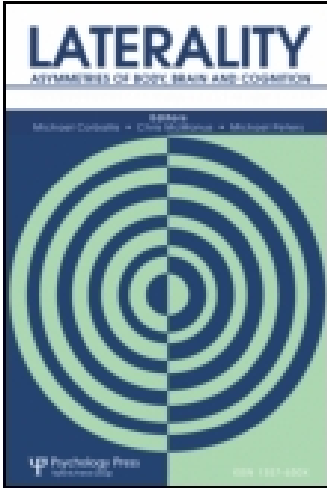
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Pawedness and Motor Asymmetries in Toads

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Pawedness was investigated in three species of toads, *Bufo bufo*, *Bufo viridis*, and *Bufo marinus*. Samples from natural populations were collected in two successive years and tested during attempts to remove a strip of paper stuck onto the snout (*Bufo bufo* and *Bufo viridis*) or during attempts to remove an elastic balloon wrapped around the head (*Bufo bufo*). A preferential right forelimb use at the population level was observed in *Bufo bufo* in both tests, whereas no clear pawedness was observed in *Bufo viridis*. *Bufo marinus* also showed no laterality in the paper-strip test, but it appeared to be strongly lateralised in another test that investigated which side the toad rotated when turned on its back underwater. Preferentially turning to the toad's left side as part of a righting response, *Bufo marinus* released the left forelimb first, using the right forelimb to control the roll to the upright position, and push to the surface. These results suggest that preferential limb use has a long evolutionary history, which dates back to early tetrapods.

INTRODUCTION

Lateral cerebral specialisation, once considered unique to humans, has been proven to exist in a variety of mammals and birds (Andrew, 1991; Bradshaw & Rogers, 1993; Denenberg, 1981; Fitch, Brown, O'Connor, & Tallal, 1993;

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Güntürkün, Emmerton, & Delius, 1989; Vallortigara & Andrew, 1994; Vauclair, Fagot, & Hopkins, 1993; Ward & Hopkins, 1993). These lateralisations are present in perceptual and motor abilities, as well as in memory formation and information processing. Recently, evidence has been accumulating that several species also show differences in the use of the limbs in some ways comparable to human handedness.

Foot use by the parrot (Psittaciformes) is a well established example of laterality in limb function at the population level, fully comparable in consistency of bias to human handedness (Harris, 1989). Friedman and Davis (1938) tested 20 parrots, of 15 different South American species, showing that they held food in their left foot on 72.2% of trials. Subsequent re-analysis of the data by Rogers (1980) showed statistically significant footedness in 7 of the 15 species, 6 being left-footed, 1 being right-footed (*Tanygnatus megalorhynchos*). Although the remaining eight species showed no obvious bias, this seemed likely to be due to too few observations (see Rogers, 1980). Rogers (1980) also studied Australian parrots, representing nine species, and found use of the left foot on approximately 90% of trials in eight species, and significant use of the right foot in one species, *Pytycerus elegans* (see also Harris, 1989). The reason why some species of parrots are right-footed while the majority are left-footed is unknown (see, however, Bradshaw & Rogers, 1993, for speculations).

Laterality in limb use has been reported in other avian species. Male goldfinches (*Carduelis carduelis*) trained to open consecutive doors for food reward used the right foot preferentially (Dücker, Luscher, & Schulz, 1986). (Goldfinches are known to use their feet to hold thistle heads when extracting the seeds with the beak, see Güntürkün et al., 1989.) Domestic chicks tested for foot use in removing a piece of sticky tape from the beak showed a strong right-foot bias; moreover, adult chickens showed a significant tendency to initiate bouts of ground scratching using the right foot (Rogers & Workman, 1993).

In rodents, lateralisation of limb use at the individual level has been reported: mice showed consistent individual preferences when tested on a task requiring them to reach into a small tube for a food reward (Collins, 1985). However, a recent report has shown lateralisation in mice at the population, not just individual, level when large samples of inbred mice are used. There was a significant right pawedness on a lateral paw preference test and left pawedness on another reaching test (Waters & Denenberg, 1994).

Even in primates, a recent reassessment of the data has shown that handedness is present in a number of species (MacNeilage, Studdert-Kennedy, & Lindblom, 1987). The lower primates seem to be left-handed for holding food, whereas the right hand is stronger and used for holding on to the tree branches. MacNeilage et al. (1987) suggested that as primates became less arboreal, the right hand became free to be used in manipulation, with a shift to right-handedness for fine motor acts (which seems to be documented in chimpanzees and gorilla, see Ward & Hopkins, 1993).

Lateralisation of brain function in mammals and in birds could be interpreted as reflecting either basic homology or parallel but independent evolutionary histories. The first hypothesis seems to be supported by recent evidence of consistent direction taken in escape turning in a species of teleost fish (*Girardinus falcatus*, Cantalupo, Bisazza, & Vallortigara, 1995), of lateralisation of vocal control systems in the frog (*Rana pipiens*, Bauer, 1993) and of aggressive responses in the lizard (*Anolis*, Deckel, 1995). Here we provide the first evidence for preferences in forelimb use at the population level in anurans.

EXPERIMENT 1

Method

The subjects used were 24 mature toads of the species *Bufo bufo*, 11 males and 13 females (mean length was 8 and 10cm, respectively), collected from a natural population (Valsanzibio, Colli Euganei, North Italy) during the spring of 1994. Toads were maintained individually in cylindrical plastic cages (20cm in diameter) and were individually isolated. Artificial light was provided for 12 hours a day. Toads were fed mealworms three times a week. They were kept in the laboratory for at least one week before testing.

At test, a small elastic plastic balloon was symmetrically wrapped around the head of the animals. Toads were then placed individually in the centre of a circular plastic tank (60cm in diameter) and the paw they used during the first attempt to remove the balloon was recorded. Use of anterior and posterior paws was recorded (test stopped after first use of one or other forelimb). Toads were given five trials in the morning and five trials in the afternoon. The entire test session was then repeated on the subsequent day. The animals were manipulated in turn by two experimenters, one right-handed and one left-handed.

Percentages of use of the right forelimb were calculated for the two daily sessions of ten trials. Significant departures from chance level (50%) were estimated by two-tailed one-sample *t*-tests. The number of animals showing prevalent (> 5) use of the right or of the left forelimb during each session of 10 trials was also considered, and differences were estimated by chi-square tests.

Results and Discussion

There were no statistically significant differences between male and female toads, $F(1,22) = 0.283$, nor any significant effects related to which experimenter manipulated the animals, $\chi^2(1) = 2.28$ n.s.

We found (Table 1) a significant preference for the use of the right forelimb to remove the balloon in the first session, $t(23) = 2.325$, $P = .029$. Fourteen animals showed prevalent use of the right forelimb during the 10 trials, and only four animals showed prevalent use of the left forelimb; use of the right forelimb deviated significantly from 1 : 1, $\chi^2(1) = 5.55$, $P = .018$.

TABLE 1
Experiment 1

	First Session	Second Session
Males (N = 11)	61.8 \pm 6.58	56.4 \pm 7.16
Females (N = 13)	56.9 \pm 4.85	53.0 \pm 6.63
Total (N = 24)	59.2 \pm 3.94	54.6 \pm 4.77

Mean percentage (\pm S.E.) of right forelimb use in *Bufo bufo* during attempts to remove an elastic balloon wrapped around the head.

Figure 1 shows the frequency distributions of forelimb use in the first session, revealing an asymmetric unimodal peak that tended to be more pronounced in females than in males.

A similar trend was present in the successive day session, but in this case the preference for the right paw was not significant, $t(23) = 0.959$, $P = .34$. Twelve animals showed prevalent use of the right forelimb during the 10 trials, and 10 showed prevalent use of the left forelimb, $\chi^2(1) = 0.18$ n.s. There was, however, a significant positive correlation between the two test sessions, $r = .49$, $n = 24$, $P = .015$.

We also recorded a limited use of the hindlimbs in attempts to remove the balloon (five animals used one of the hindlimbs in both the first and the second trial, three only in the first, and one only in the second trial). There was a tendency to use preferentially the right hindlimb, but given the paucity of data the effect was not statistically significant—mean (\pm S.E.) percentage of right hindlimb use was 63.8 ± 11.0 ; $t(8) = 1.246$, $P = .247$.

EXPERIMENT 2

Method

Another species of toad *Bufo viridis*, was studied. The subjects, collected during the spring of 1994 (Lido di Venezia, North Italy) were eight males and eight females (mean lengths 5 and 4cm, respectively). They were maintained individually in cylindrical plastic cages (20cm in diameter) and were visually isolated. Artificial light was provided for 12 hours a day. The animals were fed mealworms three times a week. They were kept in the laboratory for at least one week before testing.

As it proved impossible to find an elastic balloon of the right size for this very small-sized species of toad, a different procedure was used. A thin wet piece of paper (15 \times 4mm) was stuck vertically on to the mouth/nose regions of the animal. Each subject was placed in the middle of a circular plastic tank (60cm in diameter) and the forelimb used in the first attempt at removal of the piece of

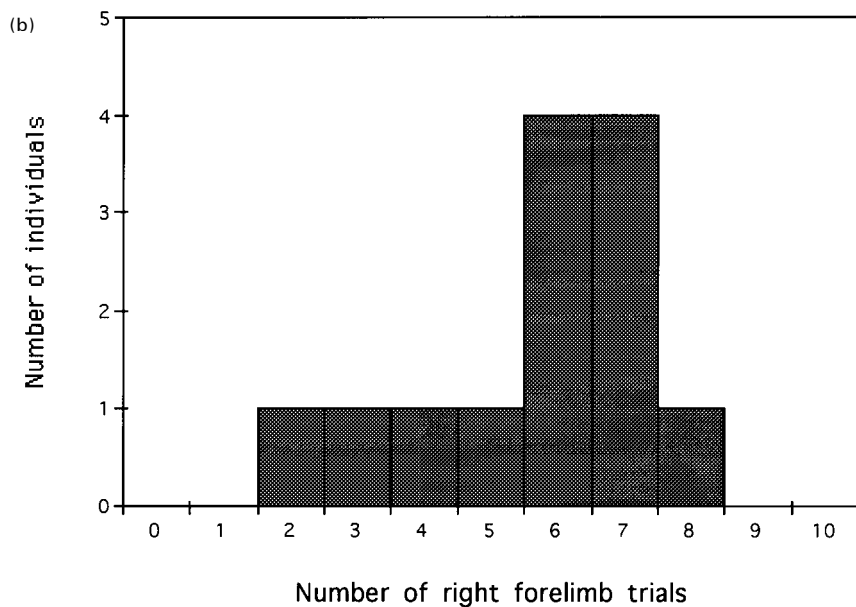
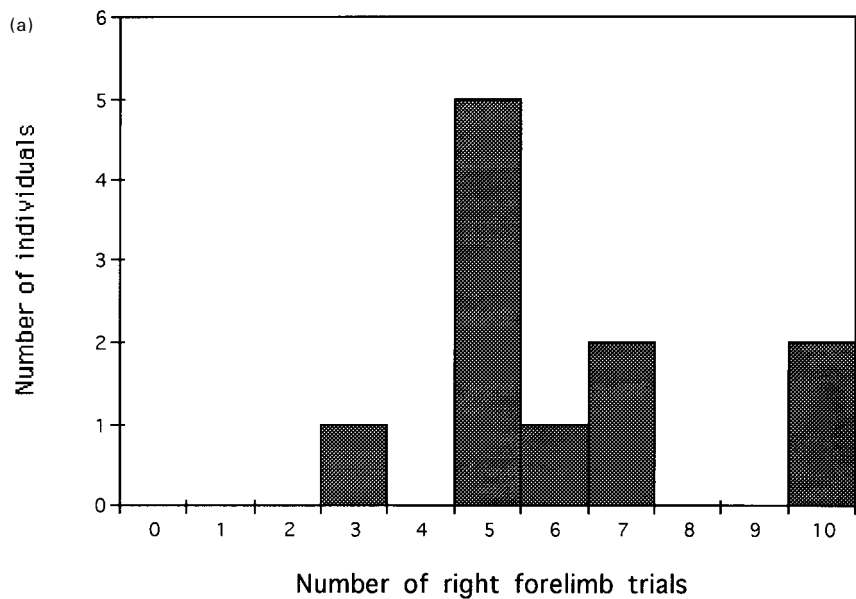


FIG. 1. Frequency distributions of right forelimb use in male (a) and female (b) toads *Bufo bufo* during attempts to remove an elastic balloon wrapped around the head (first test session).

paper was recorded. Subjects were given ten consecutive trials, during which the first forelimb used in attempts to remove the piece of paper was recorded.

Results and Discussion

There was no significant bias in the use of the forelimbs: mean right forelimb use was 51.87 ± 4.00 , $t(15) = 0.468$ n.s.; there was no difference between males and females—males 56.25 ± 6.24 ; females 47.5 ± 4.90 ; $F(1,14) = 1.21$ n.s. Seven animals showed prevalent use of the right forelimb during the ten trials, and eight animals showed prevalent use of the left forelimb, deviation from 1 : 1, $\chi^2(1) = 0.06$ n.s. No use of the hindlimbs was observed in this task.

EXPERIMENT 3

The lack of asymmetry observed in *Bufo viridis* may be due to differences in procedure, or it may represent a true species difference. As it appeared impossible to test *Bufo viridis* with a satisfactory equivalent of the balloon test, we decided to test *Bufo bufo* using the paper-strip test, re-testing *Bufo viridis* with the same procedure.

Method

The subjects used were 46 mature toads of the species *Bufo bufo*, 27 males and 19 females, and 24 mature toads of the species *Bufo viridis*, 18 males and 6 females collected during the spring of 1995 (Valsanzibio, Colli Euganei: *Bufo bufo*; Lido di Venezia: *Bufo viridis*). Toads were kept individually in cylindrical plastic cages (20cm in diameter) and were individually isolated. Artificial light was provided for 12 hours a day. Toads were maintained in the laboratory for three days before testing.

The test was similar as that used with *Bufo viridis* in Experiment 2. A thin wet strip of paper (*Bufo viridis* 15×4 mm; *Bufo bufo* 15×8 mm) was stuck vertically on to the mouth and nose regions of the animal. Each subject was placed in the middle of a circular plastic tank (60cm in diameter) and the forelimb or hindlimb used during the first attempt to remove the paper strip was recorded. A single daily session of 10 trials was given.

Results and Discussion

Results are shown in Table 2. Toads of the species *Bufo bufo* showed a significant right-forelimb preference—mean \pm S.E. percentage of right forelimb use: 55.2 ± 2.55 , $t(45) = 2.039$, $P < .05$. Twenty-six animals showed prevalent right forelimb use during the ten trials whereas ten animals showed prevalent left forelimb use, the difference being highly significant, $\chi^2(1) = 7.11$, $P = .007$.

TABLE 2
Experiment 3

	<i>Bufo bufo</i>	<i>Bufo viridis</i>
Males	53.7 \pm 3.11 (N = 27)	46.7 \pm 4.27 (N = 18)
Females	57.4 \pm 4.38 (N = 19)	50.0 \pm 2.58 (N = 6)
Total	55.2 \pm 2.55 (N = 46)	47.5 \pm 2.26 (N = 24)

Mean percentages (\pm S.E.) of right forelimb use in *Bufo bufo* and *Bufo viridis* during attempts to remove a piece of paper from the snout.

There was no significant difference between males and females in the percentages of right forelimb use, $F(1,44) = 0.492$ n.s.; see Table 2. The frequency distributions, however, suggested that female toads could be more lateralised than males (Fig. 2).

The direction of the asymmetry was the same as that observed with the balloon test (Experiment 1). When considering the overall percentage of right forelimb use in the two experiments, the departure from chance level appeared to be highly significant, $n = 70$, mean \pm S.E. = 56.6 + 2.15, $t(69) = 3.053$, $P = .0032$, with 40 animals showing prevalent right forelimb use and 14 prevalent left forelimb use, $\chi^2(1) = 12.51$, $P < .001$.

By contrast, there was no evidence of preferential limb use in *Bufo viridis*, mean \pm S.E. = 47.5 \pm 3.26; $t(23) = -0.768$. Six animals showed prevalent use of the right forelimb during the 10 trials, and eleven showed prevalent use of the left forelimb, $\chi^2(1) = 1.47$ n.s. There was no evidence of preferential limb use even when the results were considered together with those of Experiment 2, $n = 40$, mean \pm S.E. = 49.2 \pm 2.52, $t(39) = -0.298$ n.s., nor evidence of sex differences, $F(1,35) = 0.038$ n.s. The frequency distribution for the overall sample is shown in Fig. 3.

There was no use of hindlimbs observed in either species.

EXPERIMENT 4

Bufo bufo usually moved immediately after placement in the tank, walking even before starting attempts to remove the paper strip. *Bufo viridis* remained motionless and started removing attempts after this freezing reaction without any other movement in the environment. Moreover, informal observations carried out during the period of captivity revealed that *Bufo bufo* was less reactive to manipulation than *Bufo viridis*. This would point to a difference in the strength of emotional responses due to handling and (probably) catching and keeping in the laboratory between the two species. Thus, we decided to try a repeated-test experiment using a long inter-trial interval, to allow *Bufo viridis* to become accustomed to the testing situation.

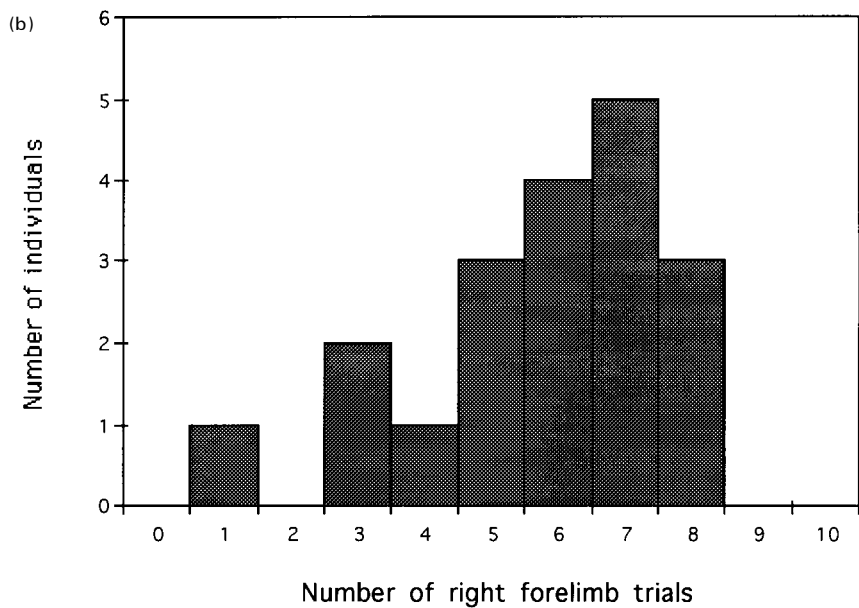
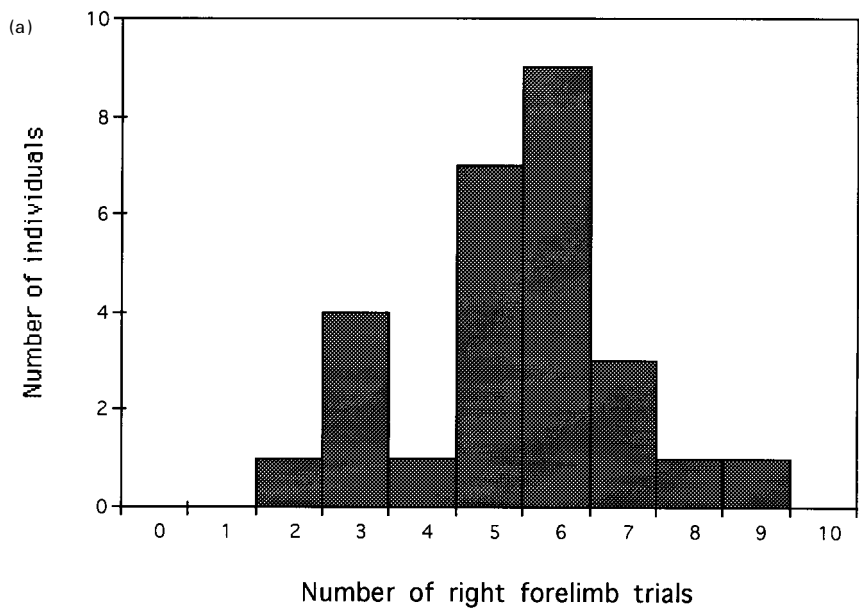


FIG. 2. Frequency distributions of right forelimb use in male (a) and female (b) toads *Bufo bufo* during attempts to remove a piece of paper from the snout.

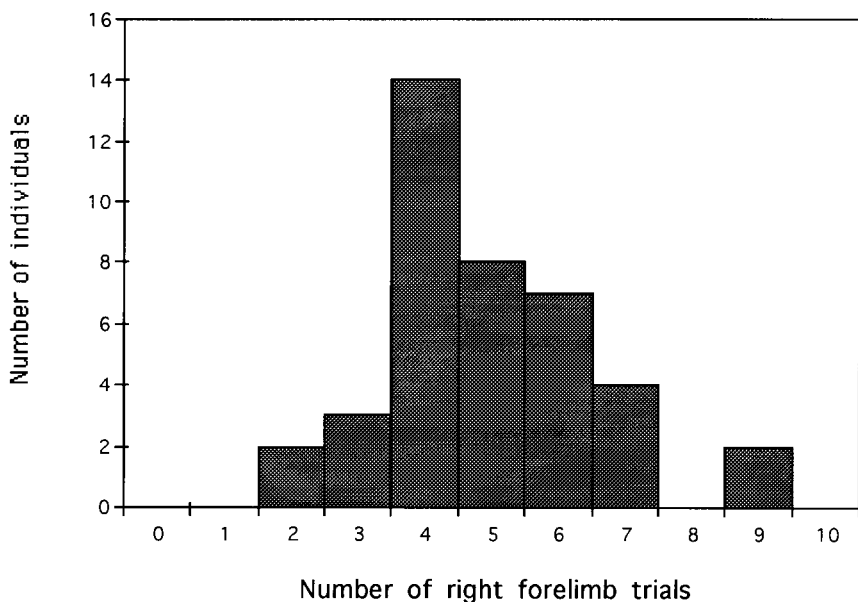


FIG. 3. Frequency distribution of right forelimb use in *Bufo viridis* during attempts to remove a piece of paper from the snout (cumulative data from Exp. 2 and Exp. 3).

Method

The subjects (collected during the spring of 1994; Lido di Venezia, North Italy) were 8 males and 9 females (4 and 5 cm in length on average, respectively). They were maintained individually in cylindrical plastic cages (20 cm in diameter) and were visually isolated. Artificial light was provided for 12 hours a day. The animals were fed mealworms three times a week.

The test, which consisted of only one daily trial, was repeated for six consecutive days. All other procedures were the same as in the previous experiment.

Results and Discussion

No clear population preference was observed (Fig. 4). There was a trend for using the left paw in the first three days (with a significant departure from chance level in the third day of test, which is however not statistically impressive because the P value should be corrected to account for repeated testing on the same group of subjects), and then a progressive shift with a preference for using the right paw.

Percentages of right forelimb use were calculated separately for the first three and the last three trials in each subject, and an ANOVA was performed on these

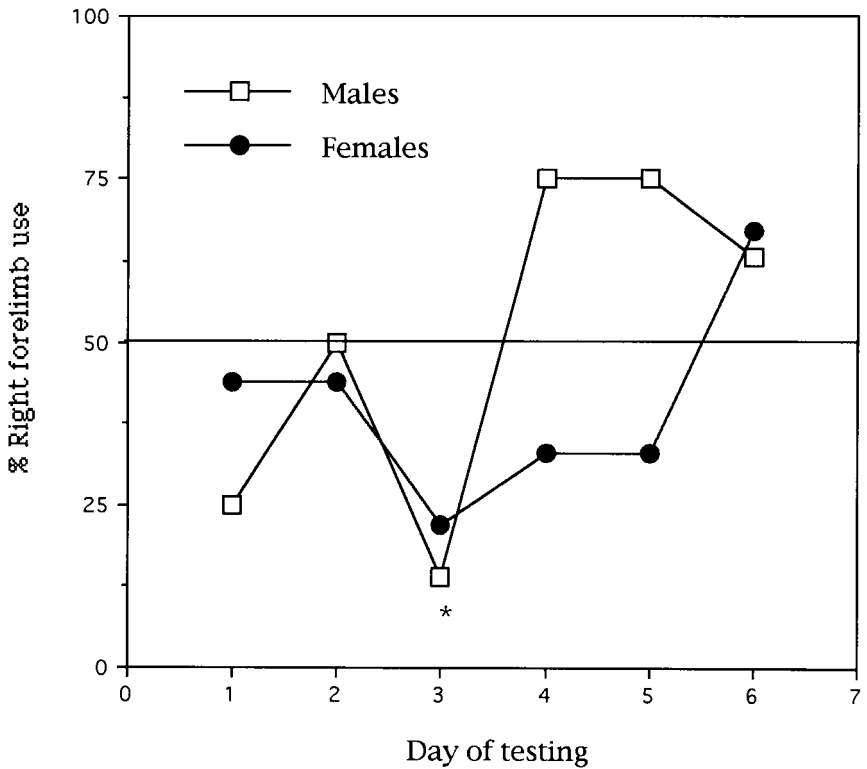


FIG. 4. Percentage of individuals using the right forelimb in attempt to remove a paper strip from the mouth in a single trial during six successive days in *Bufo viridis*. *: $\chi^2(1) = 7.11, P = 0.007$.

data, with sex as a between-subjects factor and testing time (first three, last three trials) as a repeated-measures factor. The ANOVA revealed a significant difference between the first three and the last three trials, $F(1,15) = 5.966, P = .026$. However, although the shift in bias seemed to occur earlier in males than in females (see Fig. 4), the main effect of sex, $F(1,15) = 0.572$ n.s., and the sex \times testing time interaction, $F(1,15) = 2.910, P = .105$, did not reach significance.

Overall, the results suggest that laterality in the paper-strip test in *Bufo viridis*, if it exists, is weak. Nevertheless, the different outcomes of the two testing procedures suggest that the fact that one species is not lateralised in one test does not mean that it cannot be lateralised in other tests (see Experiment 6 for more convincing evidence). The most sensible conclusion seems to be that further investigations of paw preferences in *Bufo viridis* are worth considering.

EXPERIMENT 5

Bufo marinus toads were tested for paw use in the paper-strip experiment, developed for *Bufo viridis* (Experiment 4), repeated over six consecutive days. As this species is more active at night, the toads were tested from 1800 hrs to 2200 hrs.

In early trials, *Bufo marinus* showed behaviours similar to those noted earlier for *Bufo bufo* and *Bufo viridis*. After remaining motionless, often for over 10 minutes, *Bufo marinus* toads moved about the tank before attempting to remove the paper strip. However, after several trials, most toads removed the paper strip within seconds of being placed in the tank.

Method

The subjects (collected during autumn 1995, Northern Queensland, Australia) were 11 males and 7 females (mean length 8.5cm for both sexes). They were housed in a group for at least one week before testing. Diffuse natural lighting was provided for 12 hours daily. The animals were fed *ad libitum* on cat food pellets, and were provided with mealworm larvae and beetles every three days.

Testing took place in a room kept warm, humid, quiet, and with low-intensity illumination. For each trial a paper strip (15 × 8mm) was stuck horizontally onto the mouth and nose region of the toad and the toad was then placed into the centre of a circular tank (60cm in diameter). From preliminary investigations we judged that *Bufo marinus* toads were more responsive to strips placed along the top lip rather than vertically along the median axis as used for *Bufo bufo* and *Bufo viridis*. For each daily trial, the forelimb used in the first attempt to remove the paper strip was recorded. Only once was a hindlimb used to attempt to remove the strip and it was not scored.

Results and Discussion

There was no significant bias in forelimb preference in *Bufo marinus*, mean ± S.E. = 48.2 ± 5.54; $t(17) = -0.334$ n.s., and there were no sex differences: females 50.0 ± 8.91; males 47.0 ± 7.39; $F(1,16) = 1.019$ n.s. Significant right forelimb preference during the six daily trials was shown in eight animals, and six animals showed a left paw preference, $\chi^2(1) = 1.11$ n.s. No substantial trends over the days of testing were evident.

EXPERIMENT 6

The righting reflex in frogs and toads when turned onto their backs is a behaviour described in the literature (Cogger, 1960). The animal turns either to its left or right side, and a supporting object may be used by a forelimb as leverage to assist the righting reflex. Motor asymmetries in this response were investigated in *Bufo marinus*.

Method

The inversion–submersion experiment was developed to investigate the use of the forelimbs in the righting response, and to determine if a preference for left or right forelimb use existed. The same toads used for Experiment 5 were used again for Experiment 6. Each toad was allowed to clasp the experimenter's fingers and it was then flipped along the longitudinal axis onto its back and, still clasping the experimenter's fingers, immersed in a tank of water. To avoid experimenter bias, alternate hands were used to invert each toad for every trial. The water was 10cm deep and care was taken to ensure that the sides of the tank could not be used to assist the righting response. In a videotaped experiment, the forelimb used to pivot, or roll, the toad to the righted position and the surface of the water was scored in 60 trials, 5 trials from each of 12 toads selected at random. The resultant direction taken to reach the surface (left or right of the experimenter's hand) was also scored. Only trials where both forelimbs were clasped on immersion were scored. Simultaneous release of the forelimbs, or use of the hindlimbs in the righting response, occurred infrequently (<0.5%) and these events were not included in the data.

Following the videotaped experiment, the 18 toads used for Experiment 5 were given three daily inversion–submersion trials over six consecutive days, directly following the paper-strip experiment, and were not videotaped.

Results and Discussion

From the 60 videotaped trials, rolling towards the right of the experimenter's hand occurred in 80% of the righting responses. The right forelimb was used to control the roll in 96% of these cases (15 toads were right-preferent, 2 left, 1 was ambidextrous; $\chi^2 = 9.940$, $P = .002$). Thus, simple observation of the direction in which the toad rolled away from the experimenter's hand was considered a reliable indication of forelimb preference. The correspondence between left forelimb use and left-side rolling was not so strong: 25% of rolls to the left actually used the right paw.

In the experiment with more individuals tested on 18 trials, there was a significant group bias for *Bufo marinus* to roll to the right of the experimenter's hand when completing the righting response, mean percent \pm S.E. = 66.36 ± 2.822 ; $t(17) = 5.797$, $P < .001$. There was no significant difference between the sexes: females 61.11 ± 5.686 ; males 69.70 ± 2.634 ; $F(1,16) = 1.826$ n.s., and there were no trends over the days of testing. In addition, the results for each individual were analysed separately using z -scores and only five of the eighteen toads were found to have a significant side preference ($P < .05$).

Therefore, both inversion–submersion experiments revealed a bias at the group level for *Bufo marinus* to use the right forelimb in the righting response, even when this species showed no pawedness in the paper strip experiment.

GENERAL DISCUSSION

The existence of gross morphological asymmetries at the individual level in "lower" vertebrates has always been recognised (it is common, for instance, in several species of fish, most notably flatfish, and in crabs, see Walker, 1980, and Bradshaw & Rogers, 1993, for reviews). But these morphological asymmetries bear no relation to phenomena of behavioural lateralisation such as handedness in humans or footedness in parrots. True handedness is related to lateralisation of brain function and occurs consistently in the same direction at the population level (more than 50% of individuals of the population consistently lateralised in one particular direction).

We found that two species of toad do possess a clear right forelimb bias at the population level, although this was demonstrated in different tasks. Note that toads are not individually asymmetric in their gross morphology. But we found that they have an asymmetry of function in forelimb usage at the population level.

A widespread assumption is that laterality of limb use would emerge only in those species that use the limbs for manipulative activities (Walker, 1980). Domestic chickens (*Gallus gallus*), however, which do not use the feet to pick up or manipulate objects, use the right foot preferentially to initiate ground scratching (see Introduction). Thus, it has been suggested that it is not manipulative ability alone that confers a population bias of footedness in avian species, but rather active use of the feet for feeding or searching for food (Rogers, 1989; Rogers & Workman, 1993).

Bufo bufo toads show "manipulative" use of the paws in two different circumstances. First, males, in particular, use the posterior limbs to remove other males that attempt to usurp the position on the back of the female. Unpaired males use all four legs to clasp the pairs in amplexus in the attempt to dislodge paired males. Second, males and females commonly use anterior limbs to wipe the mouth during feeding behaviour. There is a stimulus-response chain that is set in motion by a prey stimulus and which includes orienting towards the prey, binocular fixation, snapping, swallowing, and wiping the mouth with the forelimbs (Ewert, 1980). If the prey object is removed quickly during the binocular fixation, the subsequent motor patterns (including wiping) may nevertheless be carried out automatically (Ewert, 1980). This suggests that a forelimb asymmetry in wiping could be accounted for in terms of a differential involvement of the right and left sides of the brain in feeding behaviour. Forelimb use in feeding behaviours of frogs and toads has been observed in removing grass or earth from the mouth, taken in prey catching, and when pushing food well into the mouth (Cogger, 1960; Dickerson, 1906). The paper-strip test involves manipulations similar to those that may be associated with feeding, but it should also be recognised that paw use might also be grooming behaviour.

A selective involvement of the left hemisphere during feeding behaviour has been demonstrated in chickens (Rogers & Anson, 1979) and pigeons (Güntürkün & Kesh, 1987). In chickens, lateralisation of feeding behaviour has also been revealed by dominance of the right eye in tasks requiring them to search for food (Andrew, Mench, & Rainey, 1982; Mench & Andrew, 1986; Zappia & Rogers, 1987). Given this dominance of the right eye in searching for food, it makes sense that chickens have right footedness for initial scratching of the ground in searching for food. Pigeons, however, which do have a similar dominance of the right eye (Güntürkün, 1985) do not use the feet to scratch the ground during feeding (nor to wipe after feeding as do toads) and showed no footedness at either population or individual levels (Güntürkün, Kesh, & Delius, 1988). Whether toads show brain asymmetry in feeding behaviour as do chicks and pigeons remains unknown, but is worth testing.

MacNeilage (1991) has emphasised postural control specialisations in the left hemisphere as crucial in the origin of handedness in primates. Anura constitute a good example of a purely supportive forelimb, because they catch their prey with a medial organ, the tongue. However, the data reported here would suggest left forelimb support for the “wiping” test and right forelimb support for the “righting response” test.

It remains to be explained why *Bufo viridis* does not show clear pawedness. Experiment 6 suggests, however, that appropriate procedures may show this species also to be lateralised. *Bufo marinus* (Experiment 6) is, in fact, strongly lateralised in the inversion–submersion test but not in the paper-strip test. We are not aware of any data comparing the probability of forelimb use to wipe the face and mouth during feeding and grooming in the three species. We found reference to this behaviour only for *Bufo bufo* (Ewert, 1980) but we doubt that it is absent in the other two species. One difference in the eco-ethology which separates *Bufo viridis* from *Bufo bufo* and *Bufo marinus*, is the mechanism of sexual selection and pair formation, suggesting possible differences in limb usage. *Bufo bufo* and *Bufo marinus* are explosive breeders and high population densities are found in pools during the breeding season (Davies & Halliday, 1979; Straughan, 1966). In most cases *Bufo bufo* males intercept ripe females a few days before egg-laying and clasp onto the back of the females. Males are always in great excess and unpaired males try to dislodge rivals from the female’s back, engaging in struggles lasting for several hours (Davies & Halliday, 1979). In *Bufo marinus*, egg-laying is initiated almost immediately after amplexus and may only continue for a day at most (Straughan, 1975). *Bufo viridis*, by contrast, has a prolonged season and breeds opportunistically during rainy weather in temporary pools where few individuals are usually present. Male–male competition is virtually absent and pairs are formed through courtship and female choice (C. Giacoma, personal communication). This means that limb usage (during the reproductive season, at least) is much more likely to occur in *Bufo bufo* and *Bufo marinus*. It should be noted, however, that we found

a tendency for *Bufo bufo* females to be more lateralised than males, while *Bufo marinus* females tended to be less lateralised than males. Also, *Bufo viridis* may prove to be lateralised on other paw-use tasks.

To establish exactly which are the ecological variables that determine differences in the various tests will require examination of several other species of amphibians. At present, a strong case can be made from the data discussed here that lateralisation of forelimb usage could be much more ancient than anyone would have previously conceived.

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