

On the origin of skilled forelimb movements

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Homologizing behaviour was once considered unreliable, but the application of modern comparative methods has been shown to provide strong evidence of behavioural homologies. Skilled forelimb movements were thought to originate in the primate lineage but in fact are common among tetrapod taxa and probably share a common origin in early tetrapods. Furthermore, skilled movements are likely to have been derived from, and elaborated through, food-handling behaviour. In addition, it is now thought that the role played by the lateral and medial descending pathways of the spinal cord in the execution of skilled forelimb movements could be synergistic, rather than the exclusive responsibility of an individual pathway.

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SKILLED FORELIMB movements, which include the ability to reach for objects, hold them in a hand or forepaw, and manipulate them with the digits, are proposed by some authors to have developed exclusively in primates^{1,2}. Although primates are certainly skilled in the use of their forelimbs, skilled forelimb movements are also present in other mammalian^{3–6} and non-mammalian taxa⁷ (Fig. 1). Other authors have suggested that these movements are not homologous and represent convergent evolution of motor patterns that superficially resemble reaching^{8,9}. We, however, have been struck by the similarities in reaching among different mammalian taxa and suggest that the movements are homologous¹⁰. At the core of these different opinions is the issue of whether skilled movements have arisen independently within each lineage (i.e. analogy or homoplasy), or whether they have arisen early in mammalian evolution and become subsequently lost or elaborated upon in different lineages (i.e. homology)¹¹.

This is a particularly important evolutionary question in behavioural neuroscience because the overlapping patterns of behavioural and neural evolution have been frequently cited as supporting evidence for causal relationships between structure and function. For example, it has been suggested that the length and depth of penetration of corticospinal fibres are positively correlated with manual dexterity^{12,13}. Similarly, others have proposed that relative brain size and manual dexterity are positively correlated^{14–17}. One of the problems with these analyses is that they have all assumed that skilled forelimb movements have evolved independently throughout tetrapod evolution, even though the structural changes are similar. That is, because skilled forelimb movements are thought to have evolved in parallel in several different mammalian and non-mammalian taxa the neural control of the movements is therefore similar. To treat skilled forelimb movements as a homoplastic trait, rather than a homologous one, requires empirical proof that changes in the trait follow a pattern of convergence or parallelism, rather than possession of a trait held by a common ancestor¹¹. Once the homology

of forelimb movements in tetrapods has been determined, it might be possible to assess the relative importance of various selective forces and correlates with respect to their diversification.

Homoplasy or homology?

The question of homoplasy or homology is complex because there is considerable debate regarding what constitutes a homologous trait^{18,19}. For the purposes of the present analysis, we have treated skilled forelimb movements as homologous if they can be continuously traced back to a common ancestor²⁰ by mapping the presence of skilled forelimb movements on top of a phylogeny. This definition has been used in both behavioural²¹ and neural²² studies. By mapping the given traits onto a known phylogeny, the most parsimonious explanation for the distribution of character states between the species can be determined. This method can provide insight into the location and direction of evolutionary changes in a trait and the state of ancestral, or unknown, species in the lineage. This method is commonly used in evolutionary biology as a means of assessing the degree of homoplasy in a trait and whether a trait contains phylogenetic information²³. To date, such methods have been infrequently used in the neurosciences^{7,24,25} but remain a powerful means of assessing the evolution of neural structures, and the relationship between structure and function.

To fully appreciate the power of character mapping techniques, it is necessary to examine the feature of interest in as many species as possible. Skilled forelimb movements are present in frogs (Anura) and numerous mammalian taxa, therefore to discover where skilled forelimb movements first arose during vertebrate evolution, we examined the presence and absence of skilled forelimb movements in tetrapods. On the basis of observations at zoological institutions and in the laboratory, and from published reports, the major tetrapod taxa were scored for presence or absence of skilled forelimb movements (Table 1). Scoring taxa to indicate the presence of skilled forelimb movements precludes many species from being

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scored because they lack independent digits with which to grasp objects. Therefore, a second set of presence and absence scores were given whereby those species that execute the basic aspects of skilled forelimb movements, such as reaching and manipulating items without grasping, scored a presence. For example, holding beach balls between pectoral flippers in bottle-nosed dolphins (*Tursiops truncatus*) or shovelling food into the mouth with the flippers in manatees (*Trichechus* spp.) both scored a presence.

Character mapping and ancestral state reconstruction

A phylogeny of the various groups was reconstructed on the basis of a variety of recent studies on tetrapod evolution^{31–34}. Although the arrangement of some taxa might be questionable, it is important to note that different arrangements^{35–37} gave the same results.

Several different algorithms can be used to determine the most likely ancestral states of reconstructed characters^{38–40}. Two different methods were employed: maximum parsimony and unequal gains and losses. Maximum parsimony, the hypothesis that requires the fewest changes along the phylogeny¹¹, is the simplest form of character mapping and has been used in previous examinations of brain-behaviour relationships^{8,25}. It can be problematic, however, because it assumes that gains and losses of a trait are equally likely in evolution, when in fact, losses are rarely more frequent than gains^{38,39,41}. Therefore, skilled forelimb movements were assumed to be more easily lost than gained because losses appear to be related to marked changes in forelimb morphology (for example, digit fusion in ungulates) and there are no known examples of such species that have regained skilled forelimb movements.

The character mapping program, MacClade v. 3.05 (Ref. 42) was used to trace characters using both models of evolutionary change. For the unequal change model, losses were assumed to be twice as likely as gains. Identical results were produced when losses were assumed to be between 1.5 and 5.0 times more likely than gains, therefore only the twofold results will be presented.

Tracing the evolution of skilled forelimb movements

Mapping of skilled forelimb movements using maximum parsimony yielded an ancestral state of 0 for the base of the tree (Fig. 2). That is, the presence of skilled forelimb movements was absent at the base of the tetrapod phylogeny. Similarly, the bases of the Amphibia, the Reptilia and the Mammalia indicate a lack of skilled forelimb movements. Skilled forelimb movements are found in ancestral therian mammals (the marsupials and all other non-egg-laying mammals) after the branching of the monotremes (the egg-laying mammals). Absence of skilled forelimb movements in therian mammalian taxa is therefore the derived form.

When the presence of rudimentary skilled forelimb movements was mapped onto the tetrapod phylogeny, marked differences were found. For example, the ancestral state was presence (rather than absence) of skilled forelimb movements (Fig. 2). The bases of the Amphibia, Reptilia and Mammalia also indicated

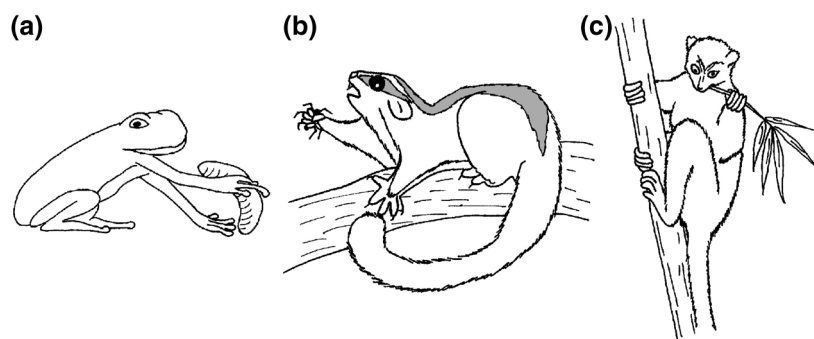


Fig. 1. Some representative examples of skilled forelimb movements in three tetrapod taxa. (a) Anura, a tree frog (*Hyla versicolor*) grasping a maggot and placing it into its mouth. (b) Marsupialia, a sugar glider (*Petaurus breviceps*) grasping an insect prior to ingestion. (c) Primates, a gentle bamboo lemur (*Haplemur griseus*) grasping and manipulating a bamboo culm.

that the presence of rudimentary skilled forelimb movements was the most parsimonious state. This suggests that skilled forelimb movements in frogs and mammals are homologous and that losses, rather than

TABLE 1. The presence or absence of skilled forelimb movements in tetrapods

Class	Order	Skilled forelimb movements ^a	Rudimentary skilled forelimb movements ^c	Refs ^d
Amphibia	Gymnophiona	0	0	–
	Urodela	ND	ND	–
	Anura	1	1	7
Archosauria	Crocodylia	1	1	e
	Aves	0 ^b	0	–
	Sphenodontia	ND	ND	–
	Sauria	1	1	26, f
	Serpentes	0	0	–
	Chelonia	0	1	f
	Monotremata	0	0	–
	Marsupialia	1	1	3, 5
	Edentata	1	1	27
	Insectivora	1	1	e
	Chiroptera	1	1	e
	Scandentia	1	1	28
	Dermoptera	1	1	29
	Primates	1	1	28
	Hyracoidea	0	0	–
	Sirenia	0	1	e
	Proboscidea	0	0	–
	Tubulidentata	0	0	–
	Macroscelidea	0	0	–
	Rodentia	1	1	6
Lagomorpha	0	0	–	
Artiodactyla	0	0	–	
Cetacea	0	1	e	
Perissodactyla	0	0	–	
Pholidota	1	1	30	
Carnivora	1	1	4	

^aThe presence of all aspects of skilled forelimb movements, reaching, grasping and manipulation, is scored as follows: 0, absent; 1, present; ND, not determined.

^bOnly one bird species, the hoatzin (*Opishocornus hoatzin*), is known to grasp with its forelimbs when young.

^cUnder this classification of skilled forelimb movements, one of the three aspects of skilled forelimb movements, reaching, grasping and manipulation, might not be present. It was scored as follows: 0, absent; 1, present; ND, not determined.

^dReferences are given for those species that scored a 1 on either of the skilled forelimb movement categories, blanks indicate no published observations.

^eUnpublished observations.

^fG.M. Burghardt, pers. commun.

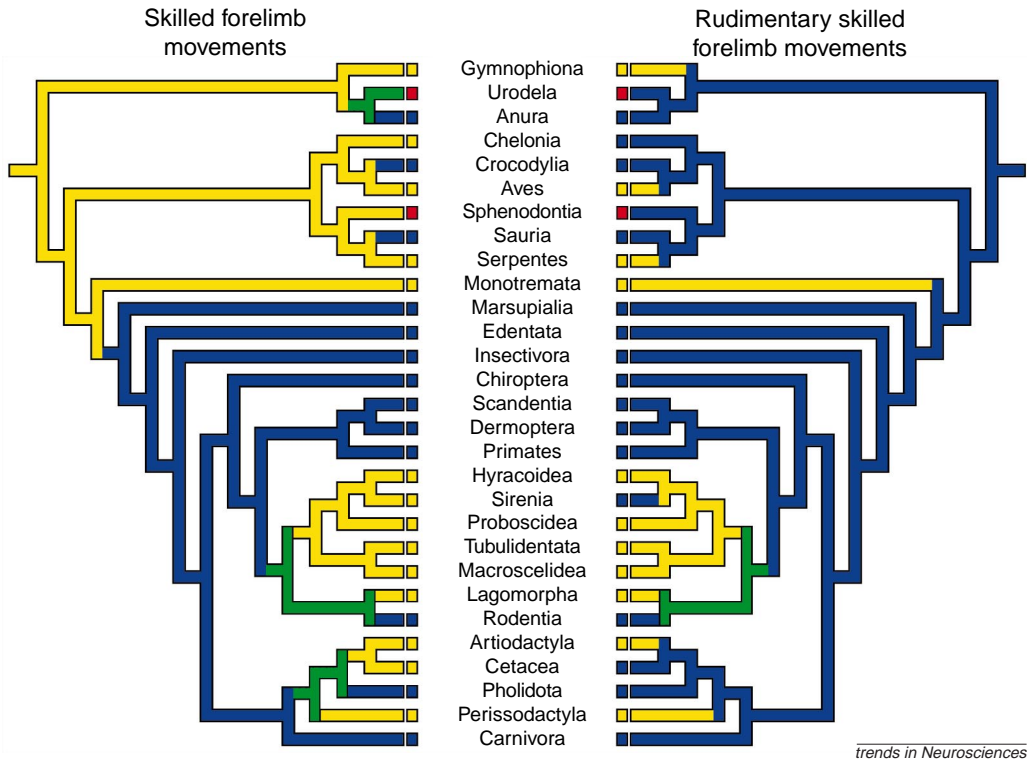


Fig. 2. The presence of skilled forelimb movements mapped onto the phylogeny of the major tetrapod taxa using maximum parsimony. Evolutionary gains are equally likely as losses in this model. The major branches indicate absence, the blue branches presence and the green branches are equivocal. Taxa shown in red indicate character states with 'unknown' scores. The break at the end of each branch is the character state of the terminal taxa and indicates the presence or absence of the trait as well as whether it is known or not.

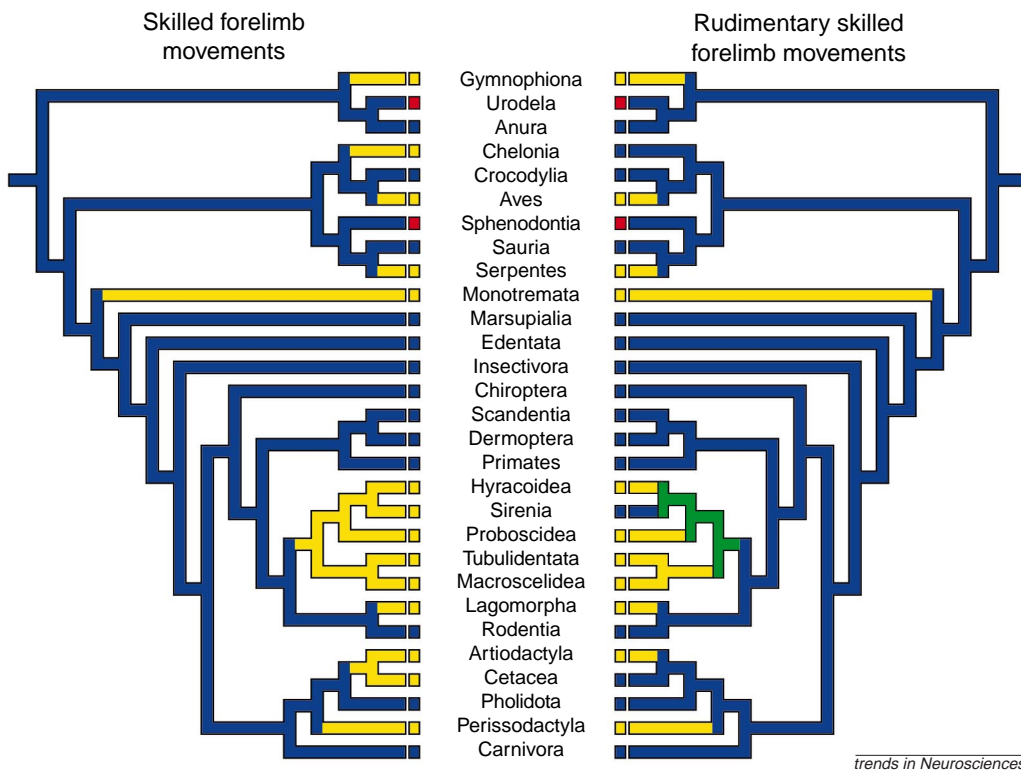


Fig. 3. The presence of skilled forelimb movements mapped onto the phylogeny of the major tetrapod taxa using an unequal gains and losses method. Using this method, losses of skilled forelimb movements are twice as likely as gains, but the same topology holds for losses that are between 1.5 to 5.0 times as likely as gains. The yellow branches indicate absence, the blue branches presence and the green branches are equivocal. Taxa shown in red indicate character states with 'unknown' scores. The break at the end of each branch is the character state of the terminal taxa and indicates the presence or absence of the trait as well as whether it is known or not.

gains, have occurred independently throughout tetrapod evolution.

With the application of the unequal model, the ancestral state of the tree was also presence of skilled forelimb movements (Fig. 3). All of the nodes were resolved and most of them were in a state of presence of skilled forelimb movements. A virtually identical pattern was produced when the rudimentary skilled forelimb movement scores were mapped (Fig. 3). Again, the ancestral state of most clades was presence.

Where did skilled forelimb movements come from?

The present analysis suggests that skilled forelimb movements are an 'ancestral' feature of mammals, and possibly tetrapods, that has its origins relatively early in evolutionary history. One intriguing question that arises from this analysis is what are skilled forelimb movements derived from? Previous investigations have suggested that they are derived from digging behaviour⁸ or locomotion⁴³. However, a close examination of frog forelimb movements involved in reaching and grasping prey suggests a different origin.

Frogs have five different types of forelimb use⁷, two of which, scooping and wiping, correspond to the definition of skilled forelimb movements used in the present study (Table 2). These two movements, plus prey stretching, offer plausible alternatives to the currently proposed origins of skilled forelimb movements^{8,43}. Prey stretching is unlikely to be the ancestral form of skilled forelimb reaching because of its use in relatively few species. The sporadic occurrence of prey stretching suggests that it is a derived behaviour, possibly related to some aspect of frog ecology⁷. Scooping and wiping, therefore, seem to be the most likely candidates for a progenitor behaviour of skilled forelimb movements. It is difficult to assess which one of these is the most likely candidate, because they are both widespread across frog species. If one assumes that the more simplistic motor pattern is the ancestral form, then scooping would be the appropriate choice. Wiping involves bringing the forelimb upwards, rotation



and finally contact with the prey item, whereas scooping does not involve a rotatory element. By contrast, wiping is occasionally present as part of the feeding repertoire in salamanders, indicating that its presence in frogs might be an ancestral feature of amphibians. Ultimately, whether scooping or wiping is the ancestral motor pattern from which skilled forelimb movements are derived is dependent upon detailed kinematic and developmental studies in amphibians.

A second alternative is to consider all these forelimb movement patterns as a continuum. That is, there might be a progressive evolution from basic aspects of locomotion (i.e. stepping) to intermediate forms of skilled forelimb movements (i.e. scooping and wiping) and finally to fully formed skilled forelimb movements. Thus, the digging and stepping proposals might not be incorrect, but simply earlier stages in the evolution of the same behavioural pattern. Nevertheless, the close relationship between particular skilled movements and feeding behaviour in many different species of animals suggests that feeding is probably related to the origin of skilled movements. Furthermore, feeding probably played a formative role in the elaboration of those movements in different orders of animals^{3,6}.

Neural control of skilled forelimb movements

Skilled forelimb movements appear to have originated early in tetrapod evolution, possibly as early as the divergence between amphibians and amniotes. This implies that various aspects of the nervous system that have traditionally been considered to be integral to the execution of skilled forelimb movements are not required. For example, the corticospinal tract (CST) has been suggested to be a crucial descending pathway from the brain, coordinating the execution of skilled forelimb movements^{12,13}. Both the depth of penetration into the spinal cord and the length of the CST fibres were suggested to be positively correlated with forelimb dexterity. The present analysis indicates, however, that even species devoid of a CST are capable of performing skilled forelimb movements. Frogs lack a CST (Ref. 44) and are not only capable of grasping prey, but also supination and placement of prey items into the mouth⁸. Thus, the CST might not be essential for producing skilled forelimb movements, a finding supported by a recent comparative analysis⁴⁵ as well as by numerous CST lesion studies in which skilled forelimb movements were impaired but not ablated^{46–49}.

An alternative descending pathway responsible for skilled forelimb movements is the rubrospinal tract (RST). The RST is present in all tetrapods, with the exception of gymnophiones and snakes, and is thought to be related to the presence of limbs or limb-like structures⁴⁵. Given that the RST innervates forelimb flexors in a similar manner to the CST (Ref. 44), it might be capable of replacing CST input to control forelimb movements^{46,47,50,51}. Three pieces of evidence indicate that the RST might not be required for skilled forelimb movements: (1) some fish possess an RST (Ref. 52); (2) it is present in many tetrapod species that do not execute skilled forelimb movements (for example, hoofed mammals); (3) sectioning of the RST (Refs 51,53), or damage to the red nucleus⁴⁹, does not ablate skilled forelimb movements.

TABLE 2. Forms of prey manipulation in frogs

Category ^a	Description
Grasping with rotation	Wrist rotates following the grasp such that the palmar surface is oriented towards the mouth.
Grasping	Digits wrap around prey and transport it into the mouth.
Prey stretching	Forepaw holds down prey as mouth grabs prey and pulls upwards.
Wiping	The palm pushes prey protruding from the mouth towards the midline.
Scooping	The digits are splayed and the back of the hand pushes prey into the mouth.

^aAll categories and descriptions are derived from Gray *et al.*⁷

This should not be taken as evidence that descending pathways are not involved in the performance of skilled forelimb movements. In fact, the presence of an RST, and not a CST, in 'early' tetrapods, such as amphibians, suggests that the evolution of the RST might have coincided with the evolution of skilled forelimb movements. Although this has not been tested in frogs, in mammals the RST appears to be important in coordinating skilled forelimb movements, but not necessarily in executing them.

Another group of descending pathways that might be important in the execution of skilled forelimb movements are the medial pathways. Both the tectospinal and reticulospinal tracts are important for motor control⁴⁴, but lesions to these medial pathways are also unsuccessful in ablating skilled forelimb movements^{53,54}. Furthermore, many aspects of skilled forelimb use are dependent upon proximal musculature that is controlled by these pathways^{48,55}.

Because lesions to any of these four descending pathways significantly affects the performance, but not the presence⁵⁴, of skilled forelimb movements the four pathways probably act synergistically to mediate skilled forelimb movements. That is, signals to the forelimbs are conducted via all four pathways and combine to execute finely coordinated skilled forelimb movements. Presumably, transection of all four pathways would lead to complete ablation of skilled forelimb movements, but this has not been determined to date.

Concluding remarks

Although the consistency of the data is suggestive of an ancestral origin of skilled forelimb movements, more research needs to be focused upon forelimb usage in non-mammalian vertebrates to give greater confidence to these results. In particular, detailed studies of forelimb use in lizards could yield insight into the neural substrates responsible for the execution of skilled forelimb movements. Once suitable data has been obtained for lizards and lesser-studied mammalian taxa, we might be better equipped to investigate neural structures that subservise skilled forelimb movements and to answer the question of where and when they first arose in tetrapod evolution. Nevertheless, we suggest that the movements have an early origin, are highly conserved, and that feeding behaviour played a principal role in their elaboration and loss in different taxa.



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