Review
Did a change in sensory control of skilled movements stimulate the evolution of the primate frontal cortex?

Ian Q. Whishaw∗
Canadian Centre for Behavioural Neuroscience, University of Lethbridge, Lethbridge, Alta., Canada, T1K 3M4

Abstract

The classical view of the evolution of such skilled movements as use of the hand and digits for reaching and grasping posited that these movements had their origin in the primate lineage. The hypothesis was that the permissive influence of adaptations to an arboreal environment led to the evolution and elaboration of these skills. Associated with skilled movements were increases in the size of the frontal lobe, temporal lobe, and cerebellum and the elaboration of new connections between these structures and other cortical regions, the brainstem, and spinal cord. The classical view saw rodents as phylogenetically old and relatively unrelated animals, displaying no skilled movements, and whose normal repertoire of behavior had little dependence on the frontal lobes. Here, evidence is reviewed that shows that the classical view of the origins of skilled movements is incorrect. Skilled movements are phylogenetically old, evolved in relation to food handling, and are especially well developed in rodents. Behavioral evidence also shows that the skilled movements of rodents are dependent upon the function of the frontal cortex. Nevertheless, there are differences in the sensory control of skilled movement in primates and rodents. Skilled movements are largely directed by vision in primates but are directed by haptics/olfaction in rodents. This difference in sensory control suggests that at a dividing point between primates and rodents, there was a profound behavior/brain transformation. Primates retained the skilled movements exemplified in rodents, but brought these movements under visual control. Correspondingly, along with many other anatomical changes, the primate frontal cortex became relatively larger and more complex under visual influence.

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Throughout most of the 20th century, primates and rodents have been seen as strikingly different in their skilled behavior. Investigators recognized that primates are able to reach for objects, grasp them with the tips of their digits, and manipulate them [55]. Most rodents were considered to have no such skills [8,54,60]. Furthermore, Napier [56] argued that rodent claws were not compatible with prehensility (one handed grasping) because claws provide a mechanical obstruction to the fingertips. Napier [56], however, allowed that some rodents, e.g. squirrels, can hold food between the palms of their forepaws as one might hold a beach ball, in this way getting around their lack of single handed prehensility. In conjunction with this classical view of the behavioral differences between primates and rodents, frontal lobe function was viewed as similarly different between the primates and rodents [8]. In the extreme, Lassak [41] argued that frontal cortex is largely dispensable in rodents. The effect of these views was that little experimental attention was paid to skilled movements in rodents. The species in this order were not seen as relevant to either the evolution of primate skilled movements or to functions of the primate frontal lobe. Furthermore, as the frontal cortex of rodents was seen as serving no special role in skilled movements, there was little investigation of the role of the frontal cortex in rodents [36].

This classical view was unfortunate for three reasons. First, rodents were neglected as a possible source of information of how the brain controls skilled movement. They were not used for studies of motor control or for investigating neurological conditions in which skilled movements are impaired. Second, because skilled movements were seen as evolving in the primate lineage, there was little study directed toward the behavioral or anatomical evolution of skilled movements in animals ancestral to the primate lineage. Thus, most studies directed toward evolution of movement skill were restricted to demonstrating relative differences in families of primates [4,21,22]. Third, the neglect of the study of skilled movements in rodents results in...
missed opportunities for understanding fundamental differences between the organization of the rodent and primate brain that distinguishes the brain/behavior relationship of both orders [26–30].

This paper reviews evidence that shows that: (1) there are structural, anatomical, and functional similarities in the limbs of rodents and primates; (2) skilled movements are phylogenetically old and evolved to subserve food handling; and (3) there are striking differences in the sensory control of skilled movements between rodents and primates. It is proposed that these similarities and differences underlie fundamental differences in brain organization between the two orders.

1. Limb structure

There are approximately two thousand species of rodents, and so this order comprises nearly one half of all mammalian species. Species within this order are adapted to aquatic, fossorial, terrestrial, and arboreal habitats. Although species within this order are distinguished by their dentition, including their continuously growing incisors, their limbs are used for a wide range of activities including hopping, running, walking, climbing, digging, swimming, and even flying. Common to most rodents is that their hind limbs provide their “motor” while the forelimbs are additionally used for support, hapsis, and skilled movements.

Obviously, there are many specializations in forelimb structure in different rodent species. Therefore, the forelimbs of a generalist, and the most studied rodent, the laboratory rat, provides reasonable summary of rodent forelimb structure. The skeletal and musculature structure of the rat forelimb is described and illustrated by Green [16]. The rat is able to generate approximately the same range of movements with a forelimb as do primates, although there are some differences in the way the movements are produced [84]. The extent of movement of the scapula is difficult to describe because there is no fixed reference point. Relative to the humerus, it can make about 10° of ventral and dorsal movement and 45° of anterior and posterior movement. It can also move together with the humerus and clavicle, which together form the shoulder joint as in primates, giving addition range of movement. The main tether of the shoulder is by muscles and they also are the main restriction on its movement. The humerus can rotate about 10°–20° in its socket with the scapula, move from 20° flexion to 108° (almost straight) in the anterior-posterior plane, and move over a one 145° range (75 medially to 75 laterally) in the mediolateral plane. The ulna and radius can make almost no rotation in their elbow joint with the humerus. At this joint they can move about 10° in the medial to lateral direction in the horizontal plane. They can flex to an angle of 10° and extend to an angle of 160° (almost straight) in the anterior-posterior plane. The paw, in relation to the ulna and radius, can rotate by about 20°, flex and extend by about 90° in each direction, and move laterally about 45° in each direction. In comparison to primates, rats have more parasagittal movement and less horizontal movement at the scapula, less rotation but otherwise similar movement at the shoulder, and more limited backward but otherwise similar movement at the elbow. Primates pronate and supinate the hand by rotating the radius over the ulna, but these bones are fused in the rat, preventing this movement. In compensation, whereas primates cannot rotate the wrist, the rat wrist is much more flexible and so can contribute the rotatory movements of the paw. In short, the forelimb of the rat is comprised of similar bones and muscles to that of primates, including humans, and with the exception of brachiating movements characteristic of apes, can make a similar range of movements.

The digits of the rat can flex and extend and open and close in much the same way that the digits of primates move. But whereas apes, including humans, can both flex and adduct the thumb, the rat seems only able to flex the thumb (digit 1). Whereas the thumb of the rat is small relative to the other digits, it is not vestigial. In addition, whereas all of the other digits have claws, the thumb has a nail, which suggests that it may be used for skilled manipulation. Digits 1 and 5 are less similar in extent, which makes it more versatile than the human small finger. Recordings of forelimb musculature in rodents, suggests that as occurs for primates, many muscle groups are active in association with most movements [24].

On the digits and paws of the rat there are pads, and these contain a rich array of sensory receptors [9]. Additionally, rats have a number of long sinus hairs on the ventral surface of the wrist, and these may be related to guiding movements and monitoring the movements of prey.

2. Motor anatomy

The neuroanatomy of the motor system of the rat has been reviewed by Wise and Donoghue [97]. In general, most of the major structures of the primate motor system are present in rodents. Thus, the rat has a motor cortex, caudate nucleus, red nucleus, and descending pathways to the spinal cord, including corticospinal tracts and a rubrospinal tracts. The corticospinal tracts of rats have their origins in three fields of pyramidal neurons in the rat, as in primates [58], and the corticospinal tracts make similar brainstem connections in rats and in primates [7,11,19,43].

Nevertheless, there are also differences in the organization of the motor system of rodents and primates. The motor cortex and the primary somatosensory cortex of the rat are overlapped rather than being separate as occurs for primates. The caudate and putamen are not separate in the rat as they are in primates. When entering the spinal cord, there are two main branches of the rat corticospinal tracts, a dorsal crossed tract and a ventromedial uncrossed tract. These pathways are likely homologous to the lateral and ventral corticospinal tracts of primates [58]. Nevertheless, whereas
the corticospinal tracts of many primates have direct connections with motor neurons of lamina IX, there appear to be few [1,43], if any, direct connections in the rat [98].

3. Skilled movements

The term skilled movements refers to movements of the limbs, paws and digits for catching, holding, and manipulating objects. Rodents use skilled movements for a number of purposes including eating, grooming, nest building, catching prey, and solving laboratory puzzles [2,6,13,14, 34,37,46,51,68]. Here description is limited to rat skilled movements, as these have received most study, including predation, food handling, and reaching for food.

Rats will hunt crickets, as will many other rodents, and they will readily learn to hunt crickets in the laboratory [25]. Once rats become experienced cricket hunters, they locate and identify crickets using audition, vibrissae palpation, and olfaction. Once it has located a cricket, a rat reaches for the cricket with a forepaw, with which it grasps and immobilizes the cricket. It then sits back on its haunches and brings up the other forepaw to assist in holding the cricket. The rat then uses the tips of its digits to manipulate the cricket so that the cricket’s head points upward. Using its mouth, the rat then removes the cricket’s head, wings, and legs, all the while manipulating the cricket with its digits. The rat then further manipulates the cricket until the cricket’s ventrum points toward the snout of the rat, which is the only part of the cricket that the rat eats. Thus, in its predatory behavior rats use a single paw for catching the cricket and use the tips of their digits for holding and manipulating the cricket so that it can be pruned and eaten. These complex paw movements may be dependent upon a sophisticated motor cortex and corticospinal projections into spinal cord interneuron pools. For example, the marsupial Monodelphis domestica, which does not have this portion of the corticospinal projection, also catches crickets with a single paw but then simply stuffs the cricket into the side of its mouth.

When picking up pieces of food, rats initially locate the food item by sniffing, and perhaps also by palpating the item using the vibrissae [82]. They then grasp the item in their mouth and sit back on their haunches to eat it. Once in a sitting posture, a rat then lifts its forelimbs, together, or one at a time, such that the paws are positioned at each side of the mouth with the palms facing medially. Using an elbows-in

Fig. 1. Shape of the digits, or digit aperture, when the paws are positioned to grasp food from the mouth (left) and when they grasp the food (right). Note that the digit aperture is adjusted relative to the size of the food before the food is grasped. Food: top, rice; middle, 500 mg food pellet; bottom, lab chow.
movement, the paws are brought toward the food so that the item can be grasped with the digit tips. In grasping the food item, the paws and digits are shaped in anticipation of the size of the item. If the item is small, the digits are flexed and closed. If the food item is large, the digits are extended and opened. It is likely that perioral sensory information is used to identify the size of the food object so that the digits can be appropriately shaped (Fig. 1). During the course of eating, the digits tips continue to manipulate the food item. In addition, the digits adopt a wide variety of postures depending upon the size and shape of food that is being handled [81].

The characteristic movements of spontaneous eating (sniffing, mouth grasping, sitting posture, elbows-in grasping, and use of the digit tips for grasping and manipulation) may well be a rodent-typical pattern, as these key movements, with some species-related modification, have been identified all rodent families [93]. The squirrel is no exception [1]. The “palm beach ball holding pattern”, described by Napier [56], included. Squirrels have an extremely large digit 1 digit tip, and it is between the tips of their thumbs and not the palm that they hold food items for eating. In addition, squirrels can hold an additional item, to the one being eaten, from between their thumbs, using the tips of their other digits [93] (Fig. 2).

Skilled reaching in the rat was first described by Peterson in an investigation of rat “handedness” [61]. He later described the importance of motor cortex for hand preference [62–65]. Subsequently, rats have been studied as they reach for food through the bars of a cage, through slots in their cage wall, out of dishes, from moving conveyor belts, and off a spinning dish [87]. The most detailed descriptions of rat reaching are given for a task in which rats reach through a slot to obtain a single food pellet located in a small indentation on a shelf [45,83,88], or down onto a staircase [96].

Rats identify food and its location by sniffing. They shift posture for a reach by using the nonreaching forepaw and its contralateral hind paw. A reach consists of at least 10 component movements. The paw is lifted from the substrate into an aiming position, in which the flexed digit tips and the elbow are aligned with the animal’s body midline (Fig. 2). When the limb is advance toward the food item the digits are extended, and then as the paw is pronated, the digits are opened. During pronation, the paw is placed over the food item using an “arpeggio” movement in which digits 5 through 2 are successively placed on the shelf [85]. The arpeggio movement positions the paw so that the palm can be used to palpate the shelf, and also so that different grasping patterns can be used depending upon the size of the food item that the paw locates. The food is grasped by flexing and closing

Fig. 2. Movement components that comprise a reach. Lifting involves lifting the forepaw, supinating the paw so that the palm faces inward and the digits are aligned with the midline of the body. Aiming involves bringing the elbow to the midline while the digits maintain their midline alignment. Advancement of the limb is produced by a movement at the shoulder and the digits are extended and the paw partially pronated. Pronation is achieved with an adduction of the elbow and rotation around the wrist, and the digits are opened for grasping. Grasp involves closing the digits around the food while flexing the wrist to lift the food. Supination occurs in two stages, in the first the paw is supinated to face the midline to be withdrawn through the slot and in the second the paw is further supinated to place the food in the mouth. Note that there is very little movement of the head and body during the reach, except that the nose is thrust into the slot to sniff the food on the first portion of the reach and then is lifted up to allow the paw to advance. Arrows indicate main movements of the relevant limb parts.
the digits and the food is lifted from the shelf as the paw is partially supinated. As the rat sits back on its haunches, the paw is further supinated to present the food to the mouth, whereupon the digits open to release the food to the mouth. The other forepaw may or may not assist in presenting the food to the mouth and in holding the food for eating.

Many of the movements and movement components describe here for the rat can be recognized in primates, including humans [89]. For example, many primates use a forepaw to catch crickets, and most use a forepaw for picking up food items. In addition, the aiming, transport, and withdrawal movements of reaching are performed mainly by upper arm movement in both rodents and primates. Rodents shape their digits in anticipation of the size of the object to be grasped, as do primates. Finally, rodents use precision grasping patterns, hold objects with the digit tips. Rodents also adjust their grasp patterns to the size and the shape of the object that is being manipulated, as do primates. Many primates use a pincer grasp, in which an item is grasped with the pads of digit 1 and digit 2, the rat also appears to use this movement pattern (Fig. 3). For example, when holding a piece of spaghetti for eating, a rat uses one paw to shovel the spaghetti into the mouth and it uses the other paw and a pincer grasp to position the spaghetti so that it enters the mouth correctly [81]. As this movement illustrates, the two paws can be coordinated in somewhat different but complementary movements, as can the paws of primates.

4. Frontal cortex damage and skilled movements

Rodent skilled movements are affected by damage to the frontal cortex and by damage to its projections to the spinal cord, and by damage to structures allied to the frontal cortex, including the lateral striatum [66,67,74], red nucleus [92,95], and cerebellum and the inferior olive [90].

In the first description of the role of frontal cortex in skilled movements, Peterson and Princard [63] noted that lesions restricted to the motor cortex resulted in reduced probability of the use of that paw for skilled reaching. Lesions to other areas of the cortex did not have a similar effect. His subsequent studies, as well as other research, indicate that if the lesion is made in the paw region of the cortex contralateral to a paw used for reaching, there is an increased probability that the animal will shift preference to its contralateral paw [64,65]. In a number of studies using success of skilled reaching as a dependent measure, it is found that there is an initial decline in success followed by considerable recovery over a 2 week postoperative period [80,87]. Recovery is not complete, however, with the residual deficit in the successful retrieval of food objects being proportional to the size of the lesion. From damage to cortical regions outside the primary motor cortex region, decreases in success are not as profound.

In contrast to the relatively preserved success displayed by rats after motor cortex damage, impairments in the qual-
Impairments that follow damage to a number of other motor system structures, including the red nucleus and pyramidal tract, may be associated with smaller reductions in success but the impairments in rotatory movements are often as profound as those following motor cortex lesions [47,48,49,77,83,86,90,100].

The quantitative and qualitative impairments in skilled movements described here for motor cortex and pyramidal tract lesions are not due to a general disruption of movement. Rats with either motor cortex lesions or pyramidal tract lesions display normal overground locomotion and ground reaction forces in overground locomotion [44,52]. Thus, the role played by the motor cortex and the pyramidal tract in the control of skilled movements is relatively specific.

A number of other lines of evidence confirm a special role for the motor cortex and the pyramidal tract in skilled movements. Electrical stimulation of motor cortex using microelectrodes elicits movements of the limb and paw of the rat. Representations of movement are found in two regions, a caudal forelimb motor region and a rostral forelimb motor region [12,17,20,57,76]. Enriching experiences, in which rats are trained to reach for food, results in increases of the distal representation of the forelimb at the cost of the proximal representation of the forelimb in both of these regions [35]. The stimulation induced movements are dependent upon the integrity of the pyramidal tract, because the movements no longer occur after pyramidal tract section [33].

5. Phylogeny

To this point, the similarities in skilled reaching between rodents and primates suggest homology rather than convergent evolution. The question of homology is complex because there is considerable debate regarding what constitutes a homologous trait [59,70]. If skilled reaching can be traced back to a common ancestor, the support for homology is strengthened. Iwaniuk and Whishaw [26] have identified a wide range of animal species that display skilled reaching. They have projected the results onto a known phylogeny in order to determine the most parsimonious explanation for these neurons are active during specific phases of the reach [6,23].

Taken together, these three lines of research in the rat, lesion, stimulation, and unit recording, converge to indicate that the frontal cortex of the rat contains at least two representations of the forelimb and that these forelimb regions regulate skilled movements. These results are much the same as those reported for primates [38,39,40], including humans [5,72]. In fact, the details of impairments observed in the rat following pyramidal tract lesions are reminiscent of the impairments observed in monkeys following pyramidal tract lesions (Fig. 4). Thus, whereas many students of primate skilled movements have emphasized that there are differences in digit control between primates and rodents, the many similarities in skilled movement control in the two orders seems appears to be just as compelling.
the distribution of the character trait. 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 [28–30]. The 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 information. To date, such methods are frequently used in the neurosciences, especially in behavioral neurosciences, but remain a powerful means of assessing the evolution of neural structures, and the relationship between structure and function.

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. A phylogeny of the various groups was reconstructed on the basis of a variety of recent studies on tetrapod evolution. Several different algorithms were used to determine the most likely ancestral states, including maximum parsimony and unequal gains and losses. The character mapping program, MACClade was used to trace characters using both models of evolutionary change. Mapping of skilled forelimb movements using maximum parsimony yielded an ancestral state of zero for the base of the tree as well as at the bases of Amphibia, Reptilia, and Mammalia. Skilled forelimb movements are found in ancestral therian mammals after the branching of the monotremes. Absence of skilled forelimb movements in therian mammalian taxa is therefore the derived form. When the presence of rudimentary skilled forelimb movements (e.g. the ability to hold an object in a forepaw) was examined, marked differences were found. The bases of Amphibia, Reptilia, and Mammalia also indicated that the presence of rudimentary skilled forelimb movements was the most parsimonious state. This indicates that skilled forelimb movements in Amphibia, Reptilia, and Mammalia are homologous, but have been lost or elaborated upon in different orders, families, and species. In addition, the ancestral state of the tree was also presence of skilled forelimb movements.

This analysis suggests that skilled forelimb movements are an ancestral feature of mammals, and possibly tetrapods, and that they had origins relatively early in terrestrial vertebrate evolutionary history. One intriguing question that arises from this analysis is what are skilled forelimb movements derived from? Previous suggestions are that they are derived from digging, climbing, or locomotion. A close examination of frog forelimb movements involved in reaching and grasping prey suggests a different origin. Frogs have five different types of forelimb use, two of which, scooping and wiping, correspond to the definition of skilled forelimb movements [15]. These two movements provide a plausible origin of all skilled 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 contact with the prey item, whereas scooping does not involve a rotatory element. 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.

The close relationship between the particular skilled movements and feeding behavior 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 [29,30]. In apes and hominids, the adaptation of skilled movements for tool use might also be considered consistent with the feeding hypothesis as the formative force in skilled movements. In these species, tool use was initially directed to food preparation or capture.

6. Implications of differences in sensory control

The evidence that skilled movements in rodents and primates are homologous and similar is compelling. Nevertheless, there are marked differences in the sensory control of skilled movements in these two orders.

Primates use vision to locate objects for which they reach and they also shape their hand to object size using visual cues. Rats apparently do not use vision to control their reaching movements. To explicitly examine sensory control of reaching in rats, Whishaw and Tomie [94] trained rats to reach for white food pellets of various sizes that were located on a black shelf. It was expected that the obvious contrast between the white pellet and the black shelf would make the food easy for a rat to see [69]. A food pellet could be obtained by reaching through one of 18 slots, and the location of the food in relation to the slot varied for each food presentation trial. A trial began when a door was raised allowing the rat to locate and reach for the food item. Its latency to locate the food, and the slots/slots through which it reached, and success were dependent measures. Once rats had mastered the task and they quickly located the food and reached only through the appropriate slot. Once optimal baseline performance was achieved, the eyes of the rats were patched so they could not see. The visually occluded animals’ performance underwent no change from baseline performance. Clearly the animals’ success did not depend upon vision. The animals then received olfactory bulb removals, and this rendered them “blind”. Their strategy then became one in which they started at one end of the shelf and reach through successive slots until they obtained a food pellet. Even with prolonged training they were unable to regain their presurgical performance.

Rats are of course not limited to using olfaction for reaching. They are able to reach for crickets with a single paw and tactile information from the vibrissae likely assists orientation in locating the cricket [25]. They also shape their digits to the size of objects that they take from their mouth. It is likely that haptic information from the perioral region pro-
vides the appropriate sensory information for digit shaping [82]. Thus, it is clear that rats (and possibly all rodents) and primates differ in a fundamental way in the sensory information that they use to identify objects for which they reach. For primates, the two important features of reaching, targeting and hand shaping, ordinarily are guided by vision. For rodents, the former movement uses olfaction and the latter movement uses hapsis. What implications do these sensory differences have for brain function?

7. Relevance of sensory control to rodent/primate differences to brain function

Contemporary evidence suggests that rodents and primates are closely related lineages and share a common ancestor [53]. The most striking neuroanatomical difference between the two orders is the dramatic increase in the relative size of the neocortex and cerebellum in primates. Jerison and others [3,31,71,75] have earlier speculated that the underlying cause of these and many other brain differences may related to visual control of behavior in primates. Previous workers, however, have not been able to specify why, of many arboreal species in various orders [26,29], including rodents, only primates would develop such dramatic anatomical changes. We suggest that it is the visual control of hand movements that is likely to be the distinguishing feature of primate behavior. The visual control of hand movements would require reorganization of the frontal lobe and other structures and well as modifications of many different associated brain structures.

The increase in frontal lobe size observed in the primate order likely derived from the many new direct and indirect connections made by visual cortex with the rest of the brain, and especially with the frontal cortex. It may also have been related to a corresponding increase in visual areas. This liberating shift in sensory control likely also resulted in a reorganization of cortical anatomy and function in which vision was preeminent. Thus, the dorsal and ventral visual streams, that control hand movements for action and for object recognition, respectively, developed as one of the overall organizing features of the neocortex of primates [50].

There are likely to be other interesting differences in anatomy and in function of the cortex of rodents and primates that relate to differences in sensory control of skilled movements. When a rat reaches for a food item, it reaches to the tip of its nose because the nose targets the item. By contrast, the primate limb is free from this constraint and can be directed over a wide angle of visual space. Single cell recording of motor neurons in primates suggest that some neurons code the force of a movement while other neurons code direction [18,19,32,73]. Because direction is monotonically coded in the rat, it would be surprising to find that rats have direction sensitive motor units. Likely their motor neurons simply code for force while the added vectorial dimension observed in primate motor units likely represents the added visual control. Stated differently, the rat frontal cortex likely represents the ancestral condition to which has been added, in primates, visual control.

Other anatomical differences between rodents and primates may also be related to the shift from nonvisual to visual control of skilled movements. The integrated sensory/motor structure of the rat forelimb motor cortex may derive from a primary role of hapsis in the control of food handling movements. With a shift to visual control, a separation of somatosensory cortex from motor cortex may have been required for vision to adopt a preeminent role. For example, in primates the major projections for primary somatosensory control are to parietal rather than to frontal cortex targets [10]. Perhaps other anatomical differences, such as the separation of the caudate/putamen also derive from visual control of skilled movements. Additionally, increases in size of the neocerebellum may be required to calibrate the direction and velocity of visually guided movements [78,99]. One of the most interesting differences between rats and primates is the paucity of direct corticomotoneuronal connections in rats versus the more plentiful direct connections in primates. This difference is generally described as being due to differences in the degree to which species in these orders can control independent digit movements [42]. Speculatively, it seems possible to suggest that differences in visual control may be contributory. Rat skilled movements appear to be acquired extremely rapidly both developmentally and during learning whereas many primate skilled movements require extensive practice and time to acquire [79]. Perhaps direct connection between the motor cortex and motor neurons are related to the extensive learning required to bring the motor system under the effective control of the visual system.

8. Conclusion

This paper has reviewed an extensive experimental literature that describes the similarities in limb structure, in anatomy, and in function of the frontal cortex of rodents and primates in the control of skilled movements. This paper also points out that there are fundamental differences in the way skilled movements are control in these two sister orders. Thus, whereas the movements themselves and the neural structures that control them may be homologous, a change to visual dominance over skilled movements in primates represents an evolutionary watershed. Many of the organizational and anatomical differences between rodents and primates may be related to this shift in sensory control. In addition, visual control of skilled movement in primates may have paved the way for the many unique behavioral and anatomical traits found in the primate order. These include increases in the number of visual areas as well as increases in the complexity of the prefrontal cortex.
References


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