

## Animal models of motor systems: cautionary tales from studies of head movement

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### Historical perspective

Studies of motor systems have always depended in large measure on the use of cats as experimental animals. Those of the head-movement system are no different. As early as the nineteenth century, experiments on decerebrate cats gave us insight into the basic reflexes and pathways responsible for the control of head movement (e.g. Sherrington, 1897; Magnus, 1926). Cats later became the animals of choice for most anatomical and electrophysiological studies of neural pathways (e.g. Wilson and Peterson, 1988; Brink, 1988), and for electromyographic studies of neck-muscle activities during head movements of different types and directions (e.g. Richmond et al., 1992; Thomson et al., 1994). However, cats are not little people. In the early 1970s, many researchers expressed concerns about the applicability of results from quadrupeds, which they believed to have horizontally oriented necks, to humans, who clearly held their heads on top of a vertically oriented cervical spinal column. It was with great relief to some that fluoroscopic studies in the early 1980s identified as misconception the view that the feline neck was oriented horizontally. Sitting and standing cats were found instead to hold their heads on a vertically-oriented upper cervical column in much the same way as

human bipeds (Vidal et al., 1986). Instead, differences were found to be present more caudally, at the cervicothoracic junction, where the vertebral column bends nearly 90 degrees, and the thoracic cord adopts a horizontal orientation (Fig. 1).

Was the new information suggesting similarities in human and feline cervical posture sufficient to allay concerns about cats as experimental models for head movement? Two problems were still to be faced. First were the obvious differences in behaviors for which the feline head appears to be adapted. The cat relies on its jaws for a diversity of tasks including fighting, killing, tearing food and carrying objects – tasks for which most humans generally use their hands. Specializations of feline neck muscles and more generally of head-movement control might be expected to enhance the performance of necessary behaviors without which the cat would be unlikely to survive. In addition, the cat is a quadruped, whose head is borne on a shoulder and forelimb system very different from that in man. As long as one believed that the head-movement system was confined to the upper cervical region, it was possible to ignore the differences below. However, we now know from EMG studies that muscles with attachments to the shoulder girdle are active during many head movements (Richmond et al., 1992; Thomson et al., 1994). We are drawn into the problem eventually faced by most motor physiologists, of where 'our' motor system ends and that of 'everyone else' begins.

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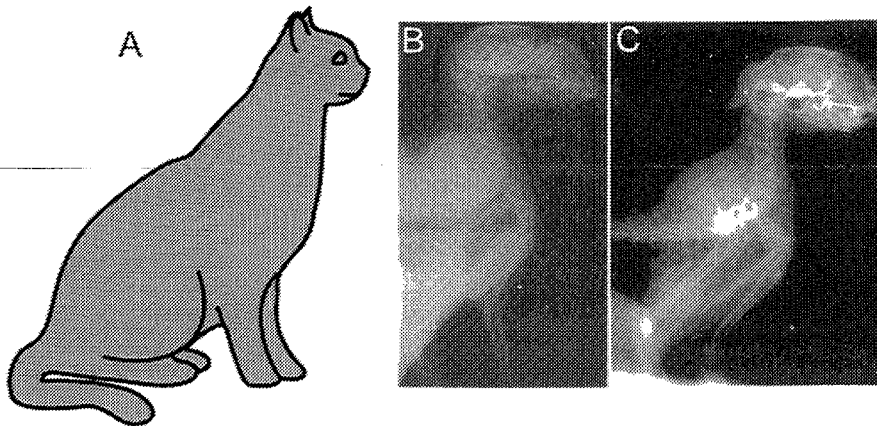


Fig. 1. Vertebral configuration of the feline neck. The outward appearance of the neck (A) belies the sharply curved cervico-thoracic region, shown in stereo X-rays (B and C). White dots in the X-rays are markers associated with a calibration device. Adapted with permission from Runciman and Richmond, 1997.

### The neck-bone's connected to the shoulder-bone

In order to understand the coupling from forelimb to neck through the shoulder, it is necessary to know the position of the feline clavicle and scapula with respect to the joints of the neck. These positions and centers of rotation determine the moment-generating capacity of several key muscles as well as the transmission of forces through the bones and ligaments of the joints themselves. To answer this question, a fluoroscopic study was carried out to identify shoulder-girdle position when the feline head and neck were held in different postures. Furthermore, by posing cats on force plates when stereo X-rays were taken (e.g. Fig. 1), data could also be used for a three-dimensional static analysis of the effects of ground reaction forces from the limbs through the various joints of the forelimb and shoulder (Runciman and Richmond, 1997). It was perhaps not surprising to find that loading on the scapula in these cursorial animals was confined primarily to the sagittal plane. What was unexpected was the rather large size of the moment in this plane that tended to rotate the vertebral border of the scapula caudovertrally with respect to the head of the humerus (counterclockwise in Fig. 2). How then can the cat sit immobile? The loading forces must be counterbalanced by a force directed cranially; we

postulated this might be transmitted by muscles linking the skull to the scapula. One candidate muscle, *rhomboideus capitis* (also called *occipito-scapularis*), is known to be active tonically when the animal adopts quietly sitting or standing postures (Richmond et al., 1992). This suggests that nature may use the weight of the head as an efficient way to counterbalance the loading forces transmitted from the paws. Does this biomechanical arrangement change the control of head movement so significantly that results from the cat cannot be used to understand human head movement?

### The feline head-neck control system

In cats, much of the research done to date has been concerned with the coordination of head and eye movements. The work suggests the presence of at least two separate brainstem systems controlling the vertical and horizontal components of combined head and eye movements in such diverse species as cats, owls and man (e.g. Hess, 1954; Isa and Sasaki, 1988; Masino and Knudsen, 1992). It also suggests substantial task-related specificity among the neck muscles. Vertical movements appear to be produced by recruiting extensor muscles containing high proportions of slow fibers. Particularly important seem to be the *biventer cervicis* (Fig. 3) and *occipitoscapularis*, which are active tonically when the head is raised or held

stationary in most postures, and which even show activity, albeit reduced activity, as the head is lowered in a controlled way from a high-held to a low-held position (Richmond et al., 1992). Muscles associated with horizontal movements, in contrast, tend to have high proportions of fast fibers (Richmond and Vidal, 1988).

However, feline head movements are important for more than watching prey; they often must also subdue it. The need for large forces, such as those employed when a cat shakes and tears prey, appears to be reflected in the adaptations of the first and second cervical vertebrae, whose dorsal and lateral processes are much larger than those typical of man (Reighard and Jennings, 1963; Selbie et al., 1993)

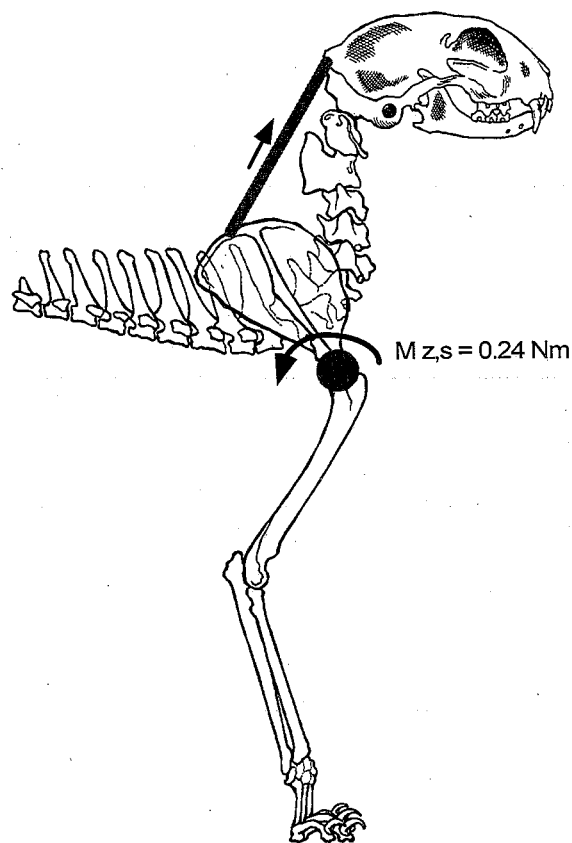


Fig. 2. Loading of the feline scapula from ground reaction forces in the sitting cat. A caudoventrally directed moment,  $M_{zs}$ , around the glenohumeral joint may be resisted by rostrally-directed forces generated in part through a muscular tether to the head. One possible tether is the muscle, occipitoscapularis, illustrated by the line joining the scapula and the skull.

(Fig. 4), and whose attached muscles have larger cross-sectional areas than allometric scaling would predict (Richmond et al., 1998). It is not yet clear whether these behaviors are controlled by the same central pathways that are responsible for the head movements in gaze. However, it is likely that their control strategies may be different from those in humans, where the head has been freed by the hands carrying out many functions for which the head must be used in carnivores.

### Non-human primates: not just scaled-up cats

The differences that seem to separate cats from humans might be avoided in experimental studies by choosing a more appropriate species, and monkeys are the most obvious candidates. Monkeys have been used extensively to investigate

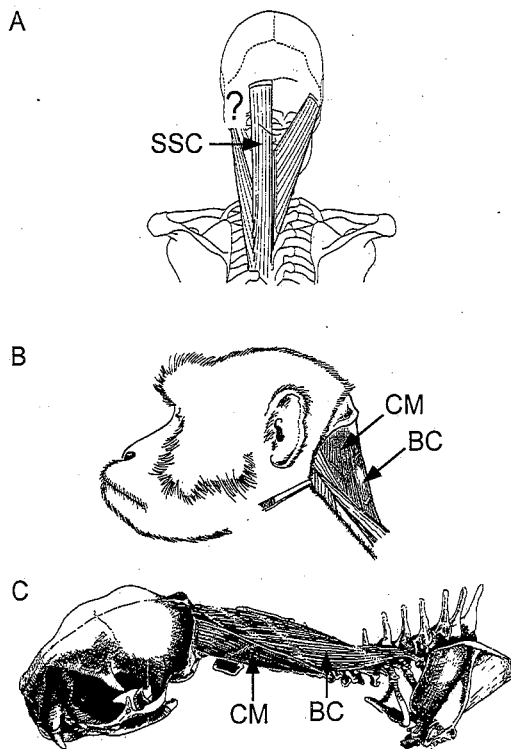


Fig. 3. Comparison of long dorsal extensors in human (A), rhesus monkey (B) and domestic cat (C). Humans have a single muscle, semispinalis cervicis (SSC), and lack a homologue to complexus (CM) (usual location marked by a question mark). Monkeys and cats have two muscles complexus (CM) and biventer cervicis (BC).

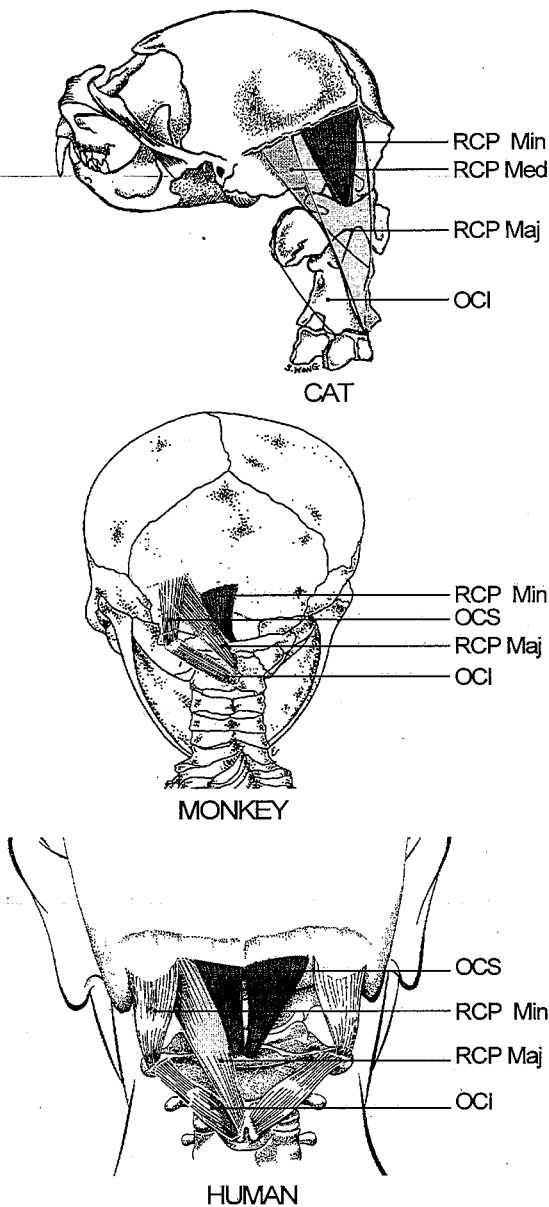


Fig. 4. Comparisons of suboccipital muscles in humans, monkeys and cats. Note the similar morphology of upper cervical vertebrae and similar relationships of suboccipital extensors in humans and monkeys. Cats have longer C1 and C2 vertebrae and a more longitudinal orientation of muscles linking the skull to C1. Adapted with permission from Kamibayashi and Richmond, 1998; Selbie et al., 1993. RCP: rectus capitis posterior; Min: minor; Med: medius; Maj: major; OCI: obliquus capitis inferior; OCS: obliquus capitis superior.

neural activity in motor systems responsible for limb and eye movements. The delays in adopting monkeys as experimental models of choice for studies of head movement may be attributed, at least in part, to the relatively poor information available about the musculoskeletal organization of the monkey neck. Further, electrophysiological studies of neural strategies are complicated by the challenges of freeing the head during recording sessions in a species not inclined to sit docilely on a platform. Head movements can interfere with microelectrode recordings from the brain and can be difficult to monitor without highly specialized equipment such as large search coils (e.g. Freedman and Sparks, 1997) or videofluoroscopy (e.g. Keshner et al., 1997).

As methods are developed to address the technical challenges of working with head-free monkeys, it is likely that monkeys will be used much more commonly because of their closer resemblance to man. Before monkeys are embraced as ideal models, however, it is important to ask whether monkeys, like cats, will be found to have specializations that may limit the applicability of experimental findings. Rhesus monkeys are the products of a different evolutionary path from that which produced cats and other carnivora (e.g. Le Gros Clark, 1962). The divergence is reflected in the bones and muscles of the neck and shoulder. Monkeys, like humans, have a shoulder girdle whose strut-like clavicle pushes the acromion of the scapula laterally and changes the sites available for attachment of the trapezius and sternomastoid muscles. Its vertebrae are also configured in ways that seem more similar to patterns in man. The C2 vertebra, for example, has a much shorter body and smaller spine than that in the cat, and this difference is associated with more human-like patterns of suboccipital muscle attachments (Fig. 4).

Between the most superficial and deep muscle layers in the monkey neck, however, there are muscles whose structures are strongly reminiscent of those observed previously in the cat. Simian dorsal extensors, for example, are relatively large and similarly structured to feline homologues. Some of this similarity may relate to the similar locomotor styles of rhesus monkeys and cats. Both

are terrestrial quadrupeds that must hold the rostrally-cantilevered head and neck in a stable position against gravitational forces. But simian muscles are not identical to those in cats either. Extensor muscles in monkeys have smaller proportions of slow fibers than homologous feline muscles, even though most other simian neck muscles have similar or higher proportions of slow fibers than feline homologues (Fig. 5). The reduced slow-fiber content may reflect the fact that monkeys walk like other quadrupeds, but sit like bipeds; their necks and backs are often held in a 'human-like' vertical orientation, in which the weight of the head is borne largely by compressive forces onto the stacked vertebrae. Regular use of such postures may reduce the need for large, tonic extensor forces and therefore may shorten the daily 'duty-cycle' of extensor muscles.

### Quadrupeds vs. brachiators

Most anthropological texts appear to share a common view that old-world monkeys such as macaques are not the direct antecedents of man but rather represent a different branch of the simian tree from which the hominids evolved. Although little is known about the comparative anatomy of their neck musculature, we might predict that the neck and shoulder anatomy of arboreal monkeys and humans will show substantial differentiation from that of macaques. Among the differences that

we might expect in man are reductions in the relative cross-sectional areas of extensor muscles in the neck and increases in the cross-sectional areas of muscles that lift and retract the shoulder.

### Human primates: not just scaled-up monkeys

At least two features of head-neck biomechanics sets humans apart from quadrupedal monkeys such as macaques. First, the center of mass of the skull is located almost directly over the cervical vertebral column rather than in front of it. Thus relatively modest forces are needed to balance the head on top of the cervical vertebral column. Second, the scapulae lie in the frontal plane. This orientation increases the range of arm movements and changes the biomechanical relationships of many muscles. The biomechanical changes are reflected in the organization of neck muscles, especially extensor muscles. For example, two differentiable muscles in the simian neck, biventer cervicis and complexus, are replaced by a single muscle in man called semispinalis capitis (Fig. 3). Further, the rhomboideus capitis muscle, which runs from the skull to the scapula in the monkey as in the cat, is no longer present in man (Kamibayashi and Richmond, 1998).

When human necks are compared to simian or feline necks, the general impression is one of structural regression. Perhaps such 'backward' change should not be too surprising. In man, head

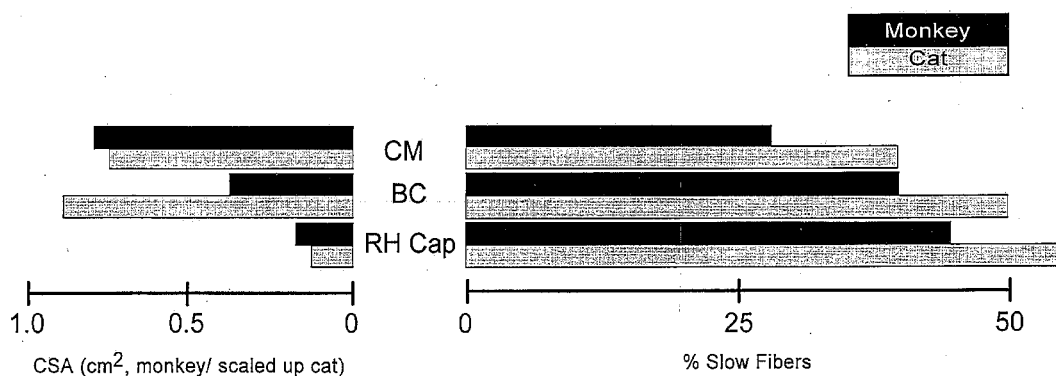


Fig. 5. Comparison of CSA and fiber-type distribution in three cat and monkey extensors, complexus (CM), biventer cervicis (BC) and rhomboideus capitis (Rhcap). To compare CSAs of extensors across species, feline muscles were scaled up by a factor of body mass<sup>2/3</sup> (1.8 × actual values). Note the relatively higher density of slow fibers in all cat muscles and the larger CSA of the chief extensor, BC. Data from Richmond and Vidal, 1988; Richmond, unpublished observations.

movements are generally used for a narrower range of purposes, to extend the visual range and orient the other sensory structures mounted on the head. Human head movements are also used expressively to convey an added dimension to the spoken word. However, all of these purposes can be achieved with relatively low levels of muscle force. The relatively low demands on the neck musculature presumably contribute to its gradual reduction in strength and complexity. This may predispose the human neck to damage and dysfunction in situations for which the neck was never adapted. Differences between the necks of humans and other animals may limit the usefulness of animal models, especially when trying to interpret the pathophysiology of common neck disorders. An understanding of the nature and extent of differences in the biomechanics of head movement may clarify both the homologies and differences in neural mechanisms for head-movement control in different species that must be used for experimental studies that cannot be carried out in man.

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