Visuomotor Coordination in Reaching and Locomotion

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Locomotion and reaching have traditionally been regarded as separate motor activities. In fact, they may be closely connected both from an evolutionary and a neurophysiological viewpoint. Reaching seems to have evolved from the neural systems responsible for the active and precise positioning of the limb during locomotion; moreover, it seems to be organized in the spinal cord. The motor cortex and its corticospinal outflow are preferentially engaged when precise positioning of the limb is needed during locomotion and are also involved during reaching and active positioning of the hand near objects of interest. All of these motor activities require visuomotor coordination, and it is this coordination that could be achieved by the motor cortex and interconnected parietal and cerebellar areas.

THE MOST BASIC MOVEMENT SYNERGY PERFORMED AT WILL is locomotion. For an animal to move from one point to another it must generate not only a propulsive thrust from limb movements or body undulations, but precise steering and equilibrium control. Land-living animals, in addition, must control the placement of the foot precisely in order to avoid obstacles that would make the animal fall over. The ability for an exact foot placement develops gradually in phylogeny. Amphibians and reptiles appear much more inexact than mammals in this respect; consider, for instance, a cat running fast and smoothly adapting to all aspects of an uneven terrain.

Visuomotor coordination in locomotion requires that the animal interpret the quality of the environment, its own position, and its speed of movement to determine when and where to put down its feet and how to integrate the control signal to each limb into the pattern of ongoing movements. It appears that the corticospinal tract of the cat is involved to a very small degree during uncomplicated movements on an even surface (*1*). However, if the requirements for exact foot placement are increased, the discharge of corticospinal neurons in the motor cortex is markedly modulated in each "step cycle," the completion of an entire step in locomotion; the more difficult the placement, the higher the degree of modulation (*1*). Ladder walking, a task requiring an exact positioning of each limb, is difficult or impossible after a transection of the corticospinal tract (*2*), although simple locomotor movements on an even surface are not affected. The corticospinal system thus appears important in locomotor control for the complex visuomotor coordination required to position the limbs, and particularly the forelimbs, appropriately. The corticospinal system appears to be involved in neither the equilibrium aspect nor the propulsive aspect, since motor cortical neurons do not change their discharge rate significantly when the equilibrium is disturbed or when the incline of the path of locomotion changes (*1*). Integration between the spinobulbar locomotor pattern generator signals to a limb (*3*) and a positioning signal from motor cortex could be achieved by just adding excitation or inhibition to an appropriate combination of motor nuclei (*3*). Exciting, for instance, all limb abductors during a step cycle would lead to a more lateral foot placement (*3*). However, it is also necessary to modify the structure of the step cycle for the animal to be able to touch ground at the appropriate instant. Thus, the spinal locomotor circuitry must also be affected. Some animals also use grasping with the paws to improve their locomotor performance, particularly when moving along difficult paths like a branch of a tree (compare cat and squirrel). The reaching and grasping ability is particularly developed in arboreal apes like the gibbons, which rapidly throw themselves from one branch to another by grasping a branch alternately with the left and right hand. This requires very precise positioning of the hand and a well-timed grasping movement.

The increasing use of the arm for accurate positioning of the hand in space independently of locomotion and of the hand for grasping and manipulation of objects is paralleled in evolution by the increasing control of these functions by suprabulbar motor structures and, in the case of the arm, by the development of specialized spinal and brainstem circuits dedicated to reaching. The main use of the arm as an independent instrument is for reaching toward objects and positioning the hand near the object. The location of the object is signaled by stimuli impinging on exteroceptive sensory systems, particularly vision. Reaching is achieved by coordinated motions at the shoulder and elbow joints, which are tightly coupled (*4*). Thus reaching can be controlled as a unit, the behavioral goal of which is to transport the hand to a desired location, just as a precise positioning movement would require. The direction of the reaching movement is more accurately controlled than its amplitude (*5*). The motor cortex is involved in the specification of the direction of reaching, as evidenced by the orderly changes in the frequency of discharge of motor cortical cells with the direction of reaching (*6*) and by the accurate prediction of this direction by populations of motor cortical neurons (*7*). Moreover, the steady-state activity of motor cortical cells is modulated in an orderly fashion with the

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active maintenance of hand position in space (*8*). This further supports the involvement of the motor cortex in the independent use of the arm, that is, for activities outside locomotion. Cells in the magnocellular part of the red nucleus are modulated with limb movements (*9*) and during locomotion (*3*), but it is not known whether these cells are also more active during walking that requires precise positioning of the limb.

The system controlling reaching and active positioning of the hand seems to comprise other major structures, including areas 2 and 5 of the parietal cortex (*10*) and the cerebellum (*11*). Both of these structures are interconnected with the motor cortex, directly (parietal cortex) (*12*) or indirectly via the thalamus (cerebellum). Moreover, the activity of cells in these areas is modulated in a fashion similar to that of the motor cortex with respect both to the direction of reaching and the active positioning of the hand in space (*10, 11*).

The contribution of motor cortex and of brain stem nuclei (for example, the red nucleus) to the initiation of reaching is channeled through an interneuronal system located above the level of proximal motor nuclei, at the C3-C4 spinal segments in the cat (*13*). These interneurons receive monosynaptic inputs from several supraspinal sources (*14*), including the corticospinal, rubrospinal, reticulospinal, and tectospinal tracts, and distribute their axons to several proximal motoneuronal pools (*15*). Sectioning the output from these propriospinal neurons to their target motoneurons results in abnormal reaching with normal grasping; similar effects are observed when the corticospinal input to the propriospinal neurons is removed (*16*). Moreover, propriospinal neurons seem to be selectively engaged during reaching movements, but are not engaged during locomotion on an even surface (*17*). However, it is probable that the C3-C4 propriospinal system would be activated in a walking task requiring accurate foot positioning, a case in which corticospinal neurons are strongly activated (*2*). Furthermore, the propriospinal neurons are phasically modulated during fictive locomotion (*18*). These results indicate that the C3-C4 propriospinal system is concerned with the neural integration of the reaching movement at the spinal level and that the motor cortex controls reaching as well as precise positioning of the limbs during walking, most probably through the C3-C4 system.

Therefore, a significant part of the neural integration of the reaching movement may be accomplished in the spinal cord, much like in locomotion (*3*). The initiation of reaching in the appropriate direction could be achieved by the activation of supraspinal motor structures, especially the motor cortex, which, in turn, would engage the spinal "reaching" circuits. The C3-C4 propriospinal neurons send an ascending collateral to the lateral reticular nucleus (*19*), which projects to the cerebellum. This pathway transmits a signal reflecting the ongoing activity in the C3-C4 propriospinal system, which could be important for the ongoing control of the evolving reaching movement by the cerebellum. In fact, the lack of coordination of arm movements observed with cerebellar lesions might be related, in part, to a lack of processing of this internal feedback signal.

In conclusion, we propose that the precise forelimb movements used to position the limb at will and to grasp different objects are very similar to, and have evolved from, those used to position the limb accurately during locomotion. Moreover, in both cases, there is a well-documented involvement of the corticospinal system (*1, 2, 6–8, 20*). We suggest that the fine control of the limb has evolved together with the system for the precise positioning of a limb during each step cycle, which is particularly developed in terrestrial mammals. The fine manipulation ability rested from early on in phylogeny (for example, fish → reptiles → cat → horse) on the control of the jaws. Only a limited number of advanced species are able to use their forelimbs for fine manipulation (compare hamsters, squirrels, and primates). This ability is linked to a type of locomotion that, in some species, requires good positioning ability of the limbs, such as in arboreal locomotion. If the control system for limb positioning is used without locomotor movements, favorable conditions are created for the development of fine manipulatory ability, given that the latter depends on precise control of positioning. In humans, in contrast to other species, the forelimbs have largely been freed from their role in locomotion and have indeed evolved to instruments for precision work (*21*).

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