Donald Lawrence and Hans Kuypers discard the long-standing notion that the pyramidal tracts have almost exclusive control of limb movements. Instead, their experiments with selective lesions make clear that the corticospinal system ‘provides the capacity for further fractionation of movements’, as exemplified by independent digit movements—at least in the monkey, whose manual dexterity is not very different from that in man.

Here, they provide one of the last pieces needed to complete the jigsaw puzzle of how the brain controls voluntary movements. The principle of crossed connections had already been recognized in antique medicine (Greek and Arabic); the crossing of motor fibres at the ventral surface of the medulla oblongata was identified by Mistichelli (1709), Pourfour du Petit (1710) and Santorini (1724); but it took almost the entire 19th century to establish the cortex as an important site of origin for fibres projecting to the opposite half of the spinal cord. Despite the work by Bouillaud (1825) and Türck (1852/3: he coined the term ‘pyramidal tract’) implicating the cortex of the frontal lobes, most neuroscientists believed that the control of movement originated in the corpus striatum. That view was eventually dispelled by Fritsch and Hitzig’s experiments with electrical stimulation in the dog (1871), Jackson’s astute clinical observations in patients with epilepsy spreading from one part of the body to another (1863) and Ferrier’s ablation experiments in chimpanzees (1871), Jackson’s astute clinical observations in patients with epilepsy spreading from one part of the body to another (1863) and Ferrier’s ablation experiments in chimpanzees (1871).

Jackson had himself already played a major role in mapping the principal anatomical connections for motor control in monkeys. These included systems originating at subcortical levels—though not in the striatum but in the brainstem. Describing the terminal distribution of the descending pathways from the cortex and brainstem in the spinal grey matter (Fig. 1), Kuypers had previously shown that corticospinal neurons arising from the precentral gyrus are distributed to the internuncial zone and the lateral motoneurons, mainly contralaterally but some ipsilaterally (Kuypers HGJM, Fleming WR, Farinholt JW. Subcorticospinal projections in the rhesus monkey. Journal of Comparative Neurology 1962; 118: 107–137). The corticospinal neurons from the postcentral gyrus terminate primarily in the nucleus proprius of the dorsal horn. The pathways arising in the brainstem are grouped into medial and lateral systems, according to their terminal distribution in the spinal cord. The lateral system, consisting mostly of rubrospinal fibres, terminates in the dorsal and lateral parts of the internuncial zone. The medial system, made up by fibres from the tectum, the interstitial nucleus of Cajal, the vestibular complex and the pontine and medullary medial reticular formation, ends mainly in the ventromedial parts of the internuncial zone. Since the terminal distributions of some corticospinal fibres are bilateral and overlap with those of the medial and lateral subcorticospinal systems, it became necessary to eliminate the influence of the corticospinal fibres on both sides in order to investigate the function of the subcorticospinal systems in isolation. This was done by sectioning both pyramidal tracts, at the upper level of the medulla oblongata. Subsequently the animals were observed in their behaviour for several weeks to months, a considerable achievement in itself, since earlier investigators reported survival periods of only a few days.

Of the 41 monkeys studied, in only 8 were the bilateral lesions of the pyramid later confirmed to have been complete, with little or no involvement of the medial lemnisci or the tegmentum. Observed immediately after surgery, these animals sat with the head up, stood, walked, ran and climbed. In contrast, in this early phase, they were unable to use the limbs—and especially the hands—indepedently from total body movements. But after some 3 weeks they reached a stage in which arm movements—in reaching for food—again became possible, though with a hooking circumduction in the shoulder and with a slightly flexed elbow. Finally, 6–8 weeks after the operation, the arm movements changed into full extension; they were also able to open and close their hands, almost independently of movements in proximal joints. By means of this grasping movement they could pick up morsels of food from the larger wells in a test board with diameters ranging from 1 to 4 cm (Fig. 2). Yet, at no time in the recovery period of up to 5 months did they manage to pick up food from the smallest holes, by means of a precision grip between thumb and index finger, as normal monkeys do (Fig. 3). All animals with pyramidal tract interruption had great difficulty in releasing the food from the hand. After unilateral pyramidotomy, the results were
similar if the unaffected arm was restrained. In a sentence prescient of the use of constraint-induced therapy, Kuypers and Lawrence remark, ‘the persistent preference for the unaffected limb required that they had to be continuously forced to use the affected extremity in order to prevent the recovered function from deteriorating’.

The companion paper reports the functional changes that occur after sectioning of either subcorticospinal system, in addition to the earlier bilateral pyramidotomy. With lesions of the medial system of descending motor pathways, the most striking abnormalities are the postural changes of the head, trunk and limbs, and a prolonged inability to right with a severe deficit in axial and proximal limb movements. At the same time, distal limb movements are considerably less impaired. Eventually, righting to a sitting position and a few unsteady steps again become possible. Lesions of the lateral brainstem pathway, in contrast, lead to severe impairment of independent use of the extremities, particularly the hands. In view of the classical nature of the ‘pyramidal’ syndrome, it is interesting that there is no mention of the term ‘spasticity’ in either of these papers.

That the capacity for individual finger movements never returns after complete interruption of the pyramidal tract is nicely in agreement with earlier anatomical studies showing that the corticospinal pathways represent the main source of descending fibres terminating directly on motoneurons, especially those innervating distal muscles, located laterally in the ventral horn. It is one of the few examples of a permanent deficit in the motor control literature. We should now attribute much recovery of other motor functions to the inherent brain plasticity, and this plasticity is clearly much reduced after complete versus incomplete lesions.

Later studies, many of them from Kuypers’ group, show that the uncrossed pyramidal fibres (ventral funiculus) terminate ipsilaterally and contralaterally on ventromedial motoneurons, which subserve axial and proximal movements. Unfortunately, some contemporary studies still conjure up the uncrossed pyramidal fibre systems to explain recovery of the distal limb function. Professor Kuypers returned from the USA to the Netherlands in the late 1960s, to establish a Department of Anatomy at the newly founded medical school in Rotterdam (now Erasmus Medical Centre). Dr Lawrence joined him there for some time, before moving in 1976 to McGill University in Montreal. Kuypers was elected to the Professorship of Anatomy at the University of Cambridge, in England, in the 1980s, where he died suddenly in 1989, at the age of 64.

Of course, these landmark studies were not quite the end of the story (see Lemon RN and Griffiths J. Comparing the function of the corticospinal system in different species: organizational differences for motor specialization? Muscle
Nor should it be assumed that the function of the corticospinal tract is purely motor; projections to the dorsal horn (from the postcentral gyrus) control afferent systems, while those to the internuncial zone inhibit spinal reflexes, monosynaptic or polysynaptic. Also, monosynaptic corticomotoneural connections result in movements only when superimposed on background activity via the internuncial zone. Finally, in man the function of subcortical systems is probably limited to axial and proximal limb movements, since some (but not all) case reports of patients with pure lesions of the medullary pyramid document permanent hemiplegia.

At one level, the function of the pyramidal tract has been overrated in that corticospinal fibres are not essential for limb movements on the contralateral side, at least in monkeys. On the other hand its function has been underrated,
since the pyramidal tract contributes uniquely to the control of individual finger movements, which, in the course of evolution, have become most developed in man (Heffner RS, Masterton RB. The role of the corticospinal tract in the evolution of human digital dexterity. *Brain Behaviour and Evolution* 1983; 23: 165–183). The result is not merely that the picking up of food has been replaced by handling cutlery, but above all that our fingers can match our cognitive abilities, be it in typing scientific articles or playing the mazurka.

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