

What studying musicians tell us about motor control of the hand

Alan H D Watson, School of Biosciences, Cardiff University, Museum Avenue
Cardiff, CF10 3US

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Summary

Most standard accounts of human anatomy and physiology are designed to meet the aims of medical education and therefore consider their subject matter from the standpoint of typical rather than outstanding levels of performance. To understand how high levels of skill are developed and maintained it is necessary to study elite groups such as professional athletes or musicians. This can lead to the rediscovery of arcane knowledge that has fallen into neglect through a lack of appreciation of its significance. For example, while variability in the muscles and tendons of the hand was well known in the nineteenth and early twentieth century, it is through recent studies of musicians that its practical significance has become better appreciated. From even a cursory acquaintance with the training methods of sportsmen, dancers and musicians it is clear that sophisticated motor skills are developed only at the expense of a great deal of time and effort. Over a lifetime of performance, musicians probably spend more time in skill acquisition than almost any other group and offer a number of unique advantages for the study of motor control. The changes in neuronal circuitry which underlie this may not only modify cortical maps but even affect the gross morphology of elements of the central nervous system. There is evidence however, that the effects of training can also be maladaptive. It appears that in some individuals, ambiguities can develop in the cortical sensory map of the hand and that this may be associated with focal dystonia; a condition to which musicians are particularly susceptible. This realisation has led to the exploration of new approaches to treatment whose benefits may ultimately extend beyond the musical profession.

Introduction

Over the last few decades, the growing interest in the biology of sporting performance in elite athletes has stimulated research in such areas as whole body physiology, tissue structure and gross anatomy and has led to significant advances both in training and the effective treatment of injury. It has made less impact in the field of neuroscience, however another elite group, instrumental musicians, has the potential to provide considerable insights into motor control and higher sensory processing. The physical challenges faced by musicians are in some respects similar to those of professional sportsmen but the biology which underlies expert musical performance has only recently come under objective scrutiny. The high level of motor control demanded of musicians in the practice of their art makes them excellent subjects for the study of skill acquisition and the exploration of the limits of performance. Indeed as a group they present some unique advantages in this regard. Many begin their

training at a very early age, often before the age of seven, when the circuitry of central nervous is still very plastic. To perform at the highest level their motor skills must be honed by many hours of daily practice, but as the activity involved is not energetically demanding, physical fatigue is not generally a limiting factor. As a consequence, intensive training can be maintained over most of a working lifespan. Practice sessions are almost entirely devoted to skill acquisition and are not diluted by the extensive periods of strength conditioning typical of athletic training. In keyboard and string players the motor activity is focused primarily on the muscles which control the hand. Stated in its crudest form, the object of the trained movements is to depress the keys or strings of the instrument with great temporal precision. These are discrete events and can provide a precise means of assessing the degree of motor control as the duration, timing and force applied can easily be measured. The fingers are mapped at high resolution in the primary sensory cortex of the brain and the hand is also well represented in the motor cortex so changes in the organisation of these regions are easy to detect against the relatively constant representations of regions of the body with contiguous cortical representations. Interestingly, in some instances these changes appear be maladaptive, and observations of the cortex of musicians suffering from focal dystonia have contributed new theories about the origin of this condition.

The object of this review is to consider some of the insights into the motor control of the hand that have been gained or placed in a clearer context by the study of musicians. The information that has emerged not only has implications for the training of musicians themselves, but also for other groups who seek to develop advanced physical skills. Being a relatively new field, it must be appreciated that the results obtained, while often tantalising, are still somewhat preliminary. The current literature, though growing steadily, is still quite small and many of the studies have involved relatively few subjects who may play a variety of instruments that make different demands on the hands. Under such circumstances, variation between subjects sometimes limits the general conclusions that can be drawn from them. For example it will become apparent that gender is a factor that needs to be taken into account in investigations of the structure and activity patterns of the central nervous system of musicians, but not all studies have done this. The review will begin by considering the constraints imposed on hand movement by the anatomy and innervation patterns of the muscles and by the interconnections between tendons. These factors are important in musicians though their significance is relatively minor in everyday life. It will then consider the process of motor learning and how cortical activity and organisation changes in relation to increasing playing proficiency. Finally it will examine a hypothesis, derived partly from the study of musicians, that the failure of motor control seen in focal dystonia is derived from maladaptive changes in cortical mapping; a notion that has suggested new approaches for the treatment of this intractable condition.

Anatomical limitations to independent finger control

The hand has evolved primarily for grasping, but in modern life it is used for a great deal more and the demands made of it in instrumental performance can push its design specifications to their limits. This is particularly marked in keyboard technique though it also applies to some extent to string and woodwind players. Standard descriptions of the actions of the muscles controlling the hand can give a misleading impression of the degree to which the fingers can be controlled individually. A number of factors conspire to limit this. For example, the individual bellies of the deep and superficial flexors and the common extensor muscles of the fingers¹ are partially fused and as a result, contraction in any one of them will result in some passive movement the others. The degree of fusion varies between individuals and in the case of the flexors, slips of muscle may even cross between the deep and superficial muscle masses. Another significant constraint is the degree to which the subdivisions of the muscle can be controlled separately by the nervous system. Studies of the deep flexor, and common extensor muscles of the fingers have revealed that there is frequently a strong synchronisation between the motor neurones² controlling the different parts of the same muscle that act on different fingers (Reilly et al., 2004; Schmied et al., 1993; Schmied et al., 2000). This is most marked for the bellies supplying adjacent fingers and is particularly strong in those acting on the ring and little fingers. With practice however, it is possible to decrease the level of synchronisation, demonstrating that the influence of the central nervous system³ can allow a greater degree finger control to be acquired. This observation is consistent with biomechanical studies of pianists which demonstrate that professionals not only exhibit more independence of finger movement than amateurs but are able to exert greater control of the duration and force of the movement (Parlitz et al., 1998). The amateurs showed a considerable degree of inappropriate co-activation not only of fingers moved by the common extensor and flexor muscles, but also between the fingers and the thumb. Whether synchrony exists between activity of motor neurones innervating muscles of the fingers and of the thumb has not been investigated physiologically, but it would not be inconsistent with what is known of descending cortical control of movement (see below).

Nineteenth and early twentieth descriptions of human anatomy paid considerable attention to anatomical variation. While variation in the paths of nerves and blood vessels which can pose problems for surgery have remained in contemporary textbooks, descriptions of variations in muscles and tendons (Bergman et al., 2004) have often been neglected. Though these may appear esoteric and of little relevance among the general population, they can be highly significant in the context of skilled movements which lie close to the bounds of what is physically possible. In some individuals, certain muscles or tendons may be absent entirely or their form or attachments may differ from the norm. For example, the superficial flexor

¹ Forearm muscles that move the fingers.

² Nerve cells in the spinal cord that control muscles of the hand via nerves running in the arm.

³ The brain and spinal cord.

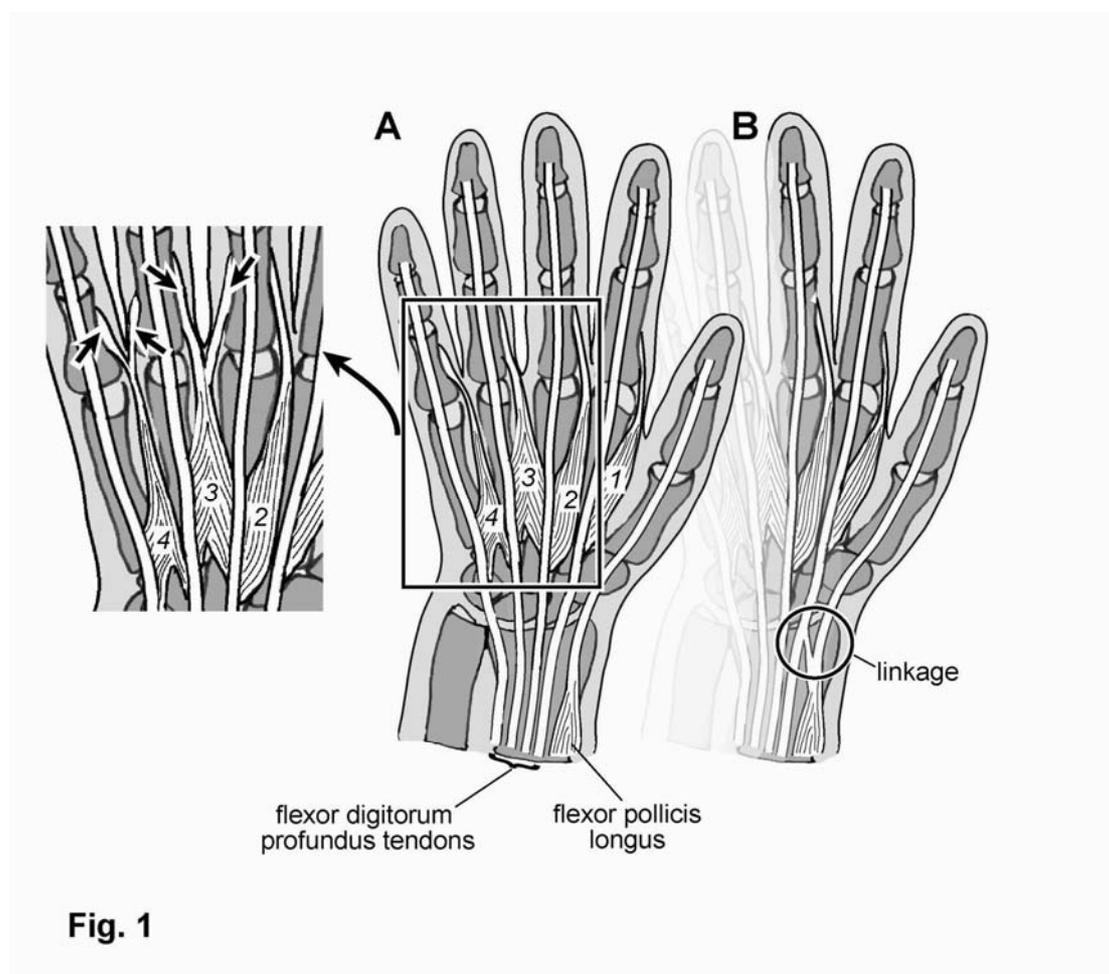


Fig. 1

Figure 1. Variability in muscle insertions and tendons of the hand. The lumbrical muscles provide one of the commonest sources of anatomical variation in the hand. The standard pattern is shown in **A** though this is probably present in less than 40% of hands. The four lumbrical muscles arise from the tendons of deep flexor muscle of the fingers and insert into the radial (thumb) side of each finger. The inset shows variations involving double tendon insertions. The incidence of these is of the order of 35-40% for the third lumbrical and 5-10% for the fourth. **B**, shows a connection between the tendons of flexor pollicis longus and the deep flexor of the index finger (Linburg-Comstock syndrome). This can cause problems for pianists in particular.

tendon to the little finger is missing in about 5% of hands (Miller et al., 2003). The intrinsic muscles of the hand make a major contribution to finger dexterity, so it is significant that variation is particularly frequent among the lumbricals (Fig. 1). These muscles allow the two terminal (interphalangeal) joints of the fingers to be straightened while the knuckle (metacarpo-phalangeal) joint is flexed. As many as 50% of hands do not show the “standard” pattern (Mehta & Gardner, 1961; Perkins & Hast, 1993). In up to a third of hands, the tendon of the third lumbrical divides to insert into both the ring and middle fingers (Fig. 1A), while in a small number of cases there is no lumbrical insertion onto the little finger at all. Therefore

regardless of the degree of training, not all musicians are capable of making the same finger movements, something that should be reflected in a flexible approach to playing technique in general and keyboard fingering in particular. Some practical examples of the problems this produces and how they be overcome are discussed by Beauchamp (Beauchamp, 2003b; Beauchamp, 2003c).

Connections between tendons running to different fingers are a significant feature of the hand. The best known example of this is the extensive pattern of linkages that exist between the tendons on the back of the hand that belong to the common extensor muscle of the fingers. This creates particular problems for independent extension of the ring finger. In addition, the tendon of extensor muscle to the little finger, which is usually entirely separate, is sometimes connected to the common extensor tendon to the little finger (Allieu et al., 1998). This makes it impossible to straighten the little finger when the others are flexed. One study has suggested that this particular anomaly is present in up to 18% of individuals while in a further 34%, the extensor muscle of the little finger may be absent entirely (Baker et al., 1981). What is less well appreciated is that within the carpal tunnel⁴, extensive connections often exist between the tendons of the deep flexor muscle of the fingers (Leijnse et al., 1997). These are either fine tendinous linkages or adherent sheets of tenosynovium⁵ both of which may be very resistant to stretch. The tensions put on these structures during playing makes them potential sites of pain and inflammation. Some attempt has been made to model the effect of such tendon linkages mathematically in the hope that this may ultimately help to identify which finger exercises are capable of improving performance and which are either useless or potentially damaging (Leijnse et al., 1992; Leijnse et al., 1993). For example, attempts to develop the ability to raise the ring finger as high as the others despite the restrictions imposed by tendon linkages may be a particular source of injury (Brown, 2000). One reason why the small intrinsic muscles are so important for hand dexterity is that they can be controlled individually to a considerable degree. Based on a knowledge of their anatomy and functional, strategies involving these muscles have been proposed by some piano teachers to minimise the impact of the limitations imposed by tendon linkages (Beauchamp, 2003a).

Though one would expect that the movements of the thumb would be quite independent of those of the fingers, it is not unusual to find an anomalous linkage between the tendon of flexor pollicis longus (a forearm muscle that flexes the thumb) and the deep flexor tendon of the index finger (Linburg-Comstock syndrome - see Fig. 1B). Various studies have suggested an incidence of between 20-35% in the general population, with about a quarter of these showing the linkage in both hands. Under these circumstances it is impossible to flex the

⁴ A channel within the wrist through which tendons pass into the palm and hence to the fingers.

⁵ Sheaths around the tendons that provide lubrication that allows them to move freely.

thumb without inducing a flexion of the index finger and in a small proportion of instrumentalists this can lead to pain or difficulty in playing (Miller et al., 2003). This is one of the few tendon linkages for which surgical section is both feasible and generally beneficial (Allieu et al., 1998).

Control of the hand by the cortex⁶

In order to appreciate the results of studies on the effect of musical performance on cortical activity, it is first necessary to understand how the cortical motor areas are organised. The notion that the primary motor cortex contains a detailed somatotopic map of the body⁷ has persisted in many textbooks despite a steady flow of evidence to the contrary (Sanes & Schieber, 2001). While there is certainly a rough somatotopic order which distinguishes regions involved in the control of muscles in the face, hand, upper limb, trunk and lower limb, detailed topographical maps cannot be identified within these subdivisions. Even Penfield, whose work is often assumed to provide one of the main bulwarks of this theory, stated that the map represented by the motor homunculus “cannot give an accurate indication of the specific joints in which movement takes place, for in most cases movement appears at more than one joint simultaneously..” (Penfield & Rasmussen, 1950; see Sanes & Schieber, 2001). Regions of cortex that can activate a particular muscle do not all lie at a single location but are scattered across a small area of motor cortex. As a result, while the area of motor cortex controlling the hand is relatively easy to define, the representations of the muscles moving different fingers or individual joints overlap to a considerable degree (Schieber & Hibbard, 1993). This would in any case be expected if only because several muscles acting primarily on the fingers not only move several joints (including the wrist), but also have slips running to more than one finger (e.g. the deep and superficial flexors and superficialis, and common extensor of the fingers). Though the muscle slips may have their own motor pools⁸, we have already seen that there can be considerable synchrony in the firing of motoneurons in different pools (Reilly et al., 2004).

Physiological studies which indicate that single pyramidal cells⁹ within the primary motor cortex can control several muscles are supported by a small number of anatomical studies providing evidence that the terminals of corticospinal neurons often end in several motor

⁶ The highly folded surface layer of the forebrain (Fig. 2). This is composed of gray matter – the nerve cells that give the brain its computational power. Regions of gray matter are linked by white matter; the cabling of the brain. The right side of the cortex controls the left side of the body and vice versa.

⁷ The cortex contains both sensory and motor somatotopic maps. In these the relative positions of different regions of the body are preserved but the maps are distorted to give a greater representation to regions that provide most sensory information or which are mostly finely controlled e.g. hands and face. The distorted body shape seen in the maps are known as the sensory or motor homunculus.

⁸ A motor pool is the group of motor neurones that supply a single muscle.

⁹ Nerve cells in the motor cortex (also known as corticospinal neurones) that extend to the spinal cord where they drive motor neurones which supply the muscles.

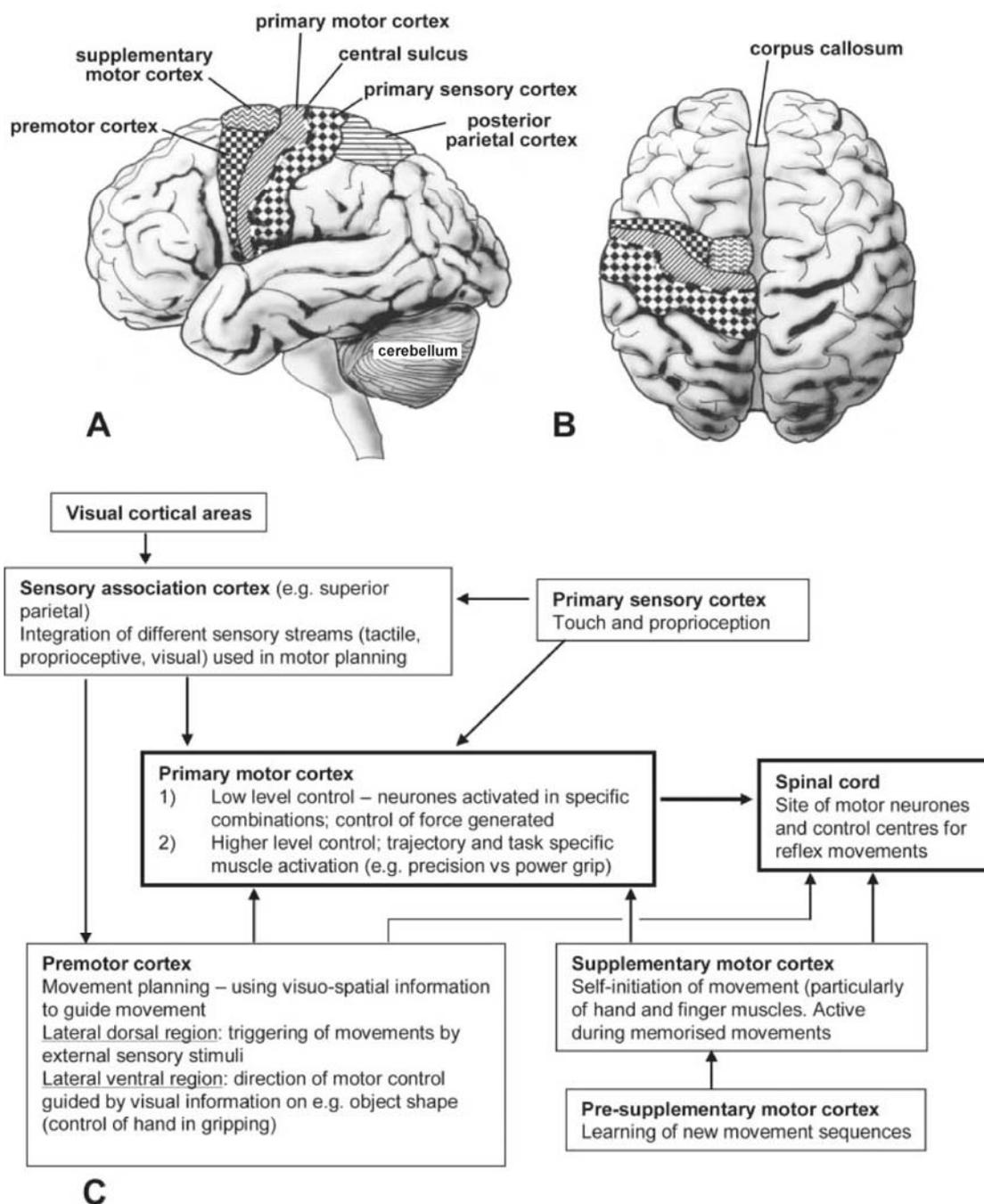


Figure 2. A, B. The cortex shown in two different views to reveal the main areas discussed in the paper. Their positions should be compared with the areas of activity shown in Fig. 3.
C. This summarizes the roles and interconnections between the areas shown in A and B.

pools, sometimes within different spinal segments (Futami et al., 1979; Kuang & Kalil, 1990; Shinoda et al., 1986). Electrical stimulation of the primary motor cortex using pulses that are longer or more intense than those needed to produce twitches in single or small groups of muscles, evokes complex but well co-ordinated movements. It appears that a given cortical neurone may drive a muscle or set of muscles only during one particular movement, and

remain silent when the same muscles are used in a different context. This has led to the hypothesis that the cortical map represents not individual muscles or joint movements but a set of limb trajectories (Graziano et al., 2002).

Activity in the primary motor cortex is driven or influenced by connections from a number of other cortical regions (Kandel et al., 2000). These regions and their inter-relationships are summarised in Fig. 2. Sensory information is received by the primary motor cortex directly from the somatosensory cortex as well as from sensory association areas such as the superior parietal region which sits immediately behind it and plays a role in integrating the sensory information used in the planning motor activity. In addition to these sensory streams, the primary motor cortex also receives inputs from several motor areas that lie just in front of it. These are principally the supplementary motor cortex and the premotor areas. Both have direct connections to the motor pools in the brainstem¹⁰ and spinal cord, so they can act on these directly as well as through the motor cortex. Like the primary motor cortex, they receive information from sensory association areas. Visual information reaches the premotor areas along two processing paths. The more ventral stream carries information on the shape and position of objects and is used to direct reaching and grasping behaviour. The more dorsal stream is active when visual and other sensory signals trigger a movement but do not guide it. The supplementary area by contrast, is concerned with movement which is self-generated rather than triggered by external cues. Into this category fall many of the movements required for playing an instrument and the finger tapping tasks discussed below in the context of motor learning. It also controls sequences of movements replayed from memory. The significance of the roles of these different motor areas in musical performance and skill acquisition will be readily apparent. When a new set of movements is first being learned, an area of the cortex that lies just in front of the supplementary motor cortex (the pre-supplementary area) is active. Though connected to it, the supplementary motor cortex is relatively silent during this initial period, but once learning has been initiated, it becomes active when the motor sequences are re-enacted. With further practice, the replaying of these sequences becomes fully automatic. The supplementary motor cortex may then fall relatively quiet again, and the activity becomes largely confined to the primary motor cortex. This posterior drift in cortical activation during learning will be encountered again when we discuss the contribution of the different motor areas of the brain in the context of musical experience.

The effect of musical performance training on cortical activation

Patterns of brain activity differ very considerably between professional and amateur musicians even when playing quite simple pieces of music. In one study, professional violinists who typically played around 30 hours a week and had an average of 30 years experience, were compared with amateurs who played only 1 hour a week and had about 10

¹⁰ The region of the brain that lies below the cortex and which is a direct continuation of the spinal cord. This contains motor neurones controlling face, tongue, larynx and throat.

years of training (Lotze et al., 2003). Their cortical activation patterns were recorded using functional magnetic resonance imaging¹¹ while they performed the left hand finger movements required to play a short extract of a Mozart concerto. Examples of these are shown in Figure 3A. As would be expected, there were many similarities between the brain responses of the professionals and the amateurs. Both showed cortical activity in primary sensory and primary motor areas that represented the hand. However, the activity in the professional group was much more tightly focussed spatially, and in the primary motor cortex was more intense and confined to the right side of the brain (the side which controls the left hand) whereas in the amateurs it was more diffuse and present on both sides. The stronger signal from the hand area of the cortex in professional group may in part be a reflection of an increase in its cortical representation (Amunts et al., 1997; Schlaug, 2001). The supplementary and premotor regions of the cortex were also active in both groups though more so in the amateurs. These regions, together with some other frontal areas, and the left side of the cerebellum¹² (the side receiving proprioceptive input [i.e. information from muscles and tendons] from the active hand) that were also active in amateurs, are involved in the acquisition of complex motor skills before they become fully automatic. In professional players therefore, it appears that many of the complex motor programmes required for executing the movements required for playing have become integrated and refined so that they arise fully formed directly from the primary motor cortex. High levels of activity in the basal ganglia¹³, which is often seen at an early stage in the formation of motor programs, was found only in the amateurs, again probably reflecting their lower level of proficiency. This may also account for the greater level of activity in the right side of the cerebellum seen in the amateurs. By contrast, in the professionals, particularly those who started their training in early life, there was an increased level of activity in a small region of the cerebellum on the same side as the active left hand¹⁴. This may be correlated with the observed structural changes seen in the cerebellum of musicians (Gaser & Schlaug, 2003; Schlaug, 2001).

Performance induced structural changes in the motor areas of the brain

Because of the great demands made on their manual dexterity, keyboard players are among the most widely studied in the search for changes in brain structure and function related to musical performance. The primary motor and sensory areas of the cortex are obvious places to search for such modifications because they contain topographical body maps in which distortions, should they exist, will be readily detectable. Most individuals show a greater dexterity with one hand or the other (i.e. they are either right or left handed) and brain imaging studies have revealed that this is reflected in the depth of the central sulcus or groove (Fig. 2)

¹¹ This allows brain activity to be revealed in awake people by identifying the areas that are taking the most oxygen from the bloodstream.

¹² A large structure on the surface of the brainstem that sits under the back of the cortex (Fig.2). It is involved in maintaining balance and plays a role in motor learning.

¹³ Large masses of gray matter that lie beneath the cortex. These ensure that different learned movements run smoothly together.

¹⁴ Unlike the cortex, the left side of the cerebellum controls the left hand

that lies along the posterior edge of the primary motor cortex on the opposite side of the brain (Amunts et al., 1996). Because there is a greater development of grey matter within the primary motor cortex on the side controlling the dominant hand, it bulges out more, making the sulcus deeper. Left/right asymmetry is seen only in the hand region of the primary motor cortex, and not in the part lying immediately below it, which controls the muscles of the face. The playing of keyboard instruments requires an almost equal dexterity in both hands so it has been proposed that the difference between the depth of the central sulcus on the left and right side should be less in keyboard players than in the general population. This indeed appears to be the case, at least for male players (who are the only group studied so far) and can be attributed to the greater development of the motor cortex on the side controlling the non-dominant hand (Amunts et al., 1997; Schlaug, 2001). This anatomical observation correlates with a greater symmetry in finger dexterity between the two hands in pianists (Jancke et al., 1997). The depth of the sulcus on both sides of the brain of keyboard players shows some correlation with the age at which they started to learn to play. There was no association with the total number of years of playing at the time the study was carried out, indicating that the morphological changes reflect a plasticity in brain structure which occurs only early in life.

The two cerebral hemispheres¹⁵ are linked by a large bundle of transverse fibres known as the corpus callosum (Fig. 2) and it might be envisaged that the requirement to coordinate the two hands in instrumentalists would lead to changes in its structure. The corpus callosum matures slowly. Though it grows most rapidly in the first decade of life it continues to increase in size until the mid twenties. The period of most rapid growth coincides with time in early childhood when motor coordination is developing. Sensory deprivation during this period can result in a reduction in the size of parts of the corpus callosum. A comparison has been made between the size of the callosum in a population of musicians and one of non-musicians in the 18-35 year age range. In two separate studies of different groups of male musicians the anterior part of the corpus callosum was found to have a greater area than in the control groups (Lee et al., 2003; Schlaug et al., 1995). This region carries connections between the primary sensory and primary motor areas on each side of the brain, as well as between the premotor and supplementary motor regions. Its larger size in musicians might therefore be linked to the observed changes in the primary motor cortex already discussed. When the motor cortex on one side of the brain is active, the equivalent region on the opposite side is usually inhibited. In pianists and guitarists it has been reported that this inhibition is reduced but is it unclear if or how this is related to the changes in the corpus callosum. It has been hypothesised this may improve the ability to coordinate the precise timing of the movements of the two hands (Nordstrom & Butler, 2002; Ridding et al., 2000). In contrast to the situation seen in male musicians, one study involving female musicians has suggested that they show

¹⁵ The cortex is divided into two symmetrical halves or hemispheres.

no increase in the dimensions of the corpus callosum compared to a control group of non-players (Lee et al., 2003).

Since the middle of the nineteenth century, the cerebellum has been associated with the control of motor activity and motor learning (Parsons, 2003). Imaging studies of the cerebellum in living subjects have revealed that its volume (as a percentage of total brain volume), appears greater in male instrumentalists than non-musicians (Schlaug, 2001). Interestingly, unlike some other morphological changes, this is said to be related not to the age at which music training began but to the intensity of current long-term practice (Hutchinson et al., 2003). The timescale over which this volume change takes place is unknown. The bulk of the cerebellum is made up of white matter, however it appears that the increase in cerebellar volume is not due to an increase in this alone. The relative size of the region of the cerebellar cortex involved in control of the left hand is also positively correlated with the degree of musical training (Gaser & Schlaug, 2003). As all of the musicians in this study were right handed this represents an increased representation of the non-dominant hand. The situation in females is different however. Relative to overall brain volume, the dimensions of the female cerebellum appear comparable to that of the male musician group regardless of musical experience.

Learning to play the music

Developing the skills to play a musical instrument proficiently involves a variety of learning tasks. First it is necessary to learn how to produce the sound and finger the notes. For a first instrument, this is generally runs in parallel with acquiring the cognitive ability to read musical notation and the two tasks must be brought seamlessly together so that seeing a note or group of notes on the stave automatically leads the fingers to make the correct movement. The motor behaviour is gradually refined to increase the speed and accuracy of execution so that the sound generated meets the expectations of the player and audience. By the age of twenty, an expert player will typically have accumulated in the order of 10,000 hours of practice (Sloboda et al., 1996). Very high levels of control are required not only for accurate rendition of the music, but also to enable it to be played with expression – a rather intangible but generally instantly recognisable element of performance which is realised by subtle manipulation of timing and dynamics.

The mechanism of motor learning

The studies that are of most relevance to understanding how the technical ability to play an instrument is acquired, or how the performance of a previously unknown piece of music is brought to perfection, are based on the learning of simple patterns of finger movement. Several investigations use a task which requires that the pads of different fingers be brought into contact with that of the thumb in a particular sequence. The subjects are asked to do this as rapidly and as accurately as possible without looking at the hand. The results suggest that

we learn to carry out such patterns of movement in several stages (Karni et al., 1995; Karni et al., 1998). An initial phase of fast learning takes place over a period of minutes during which there is a significant improvement in performance, however this is followed by a subsequent period of consolidation lasting six to eight hours which continues in the absence of the activity. Thus when the task is repeated (for example, the next day) there has been a further improvement in performance beyond the final level achieved at the end of the first practice session. During the next few weeks, daily practice sessions produce additional improvement but these increments become progressively smaller until an upper level of proficiency is reached. To break through this ceiling then requires a considerable increase in effort. Some notions of the mechanisms underlying these processes have been gleaned from imaging brain activity during this type of learning. When the task is carried out for the first time, activity is seen in the primary motor cortex controlling the active hand. When repeated, the level of cortical activity is initially reduced due to habituation, but when the finger sequence has been repeated many tens of times, the signal in the cortex becomes larger, and then remains at this level during subsequent training sessions. It is during this latter stage of motor learning that the new synaptic connections¹⁶ are made that underlie the reorganisation of the motor cortical map (Kleim et al., 2004). Of course as we have already seen, the primary motor cortex is not the only part of the brain which is involved in motor learning. Activity is also present in areas such as the premotor and supplementary motor cortex, as well as in the basal ganglia and the cerebellum (Hund-Georgiadis & von Cramon, 1999). Activity in subcortical structures occurs particularly during the early phases of motor skill acquisition and declines as greater competence is achieved.

Significantly, it has also been shown that cortical activity during the initial stages of learning of finger tapping tasks differs between pianists and non-musicians. In pianists there is much less activity in the supplementary motor and premotor areas, and greater activity in the primary motor cortex (Haslinger et al., 2004). Right from the outset, the pianists appear to be showing a pattern of activity that the non-musicians take some time to develop, which presumably reflects their previous intensive training in the control of fine finger movement. The supplementary motor cortex is thought to be involved in the control of sequential movements carried out in the absence of visual feedback. It is more active when the task is complex and so the reduced activity in this region in the pianists may imply that the task is less demanding for them. These differences in the patterns of cortical activity resemble the ones we have already seen between amateur and professional musicians (Lotze et al., 2003) (Fig. 3A,B).

Though the left side of the brain controls the right hand and vice versa, there is some evidence that training of the non-dominant hand may also cause activation of the other motor cortex. This suggests that training one hand may improve the performance of the other one

¹⁶ Synapses are the connections through which nerve cells communicate with each other .

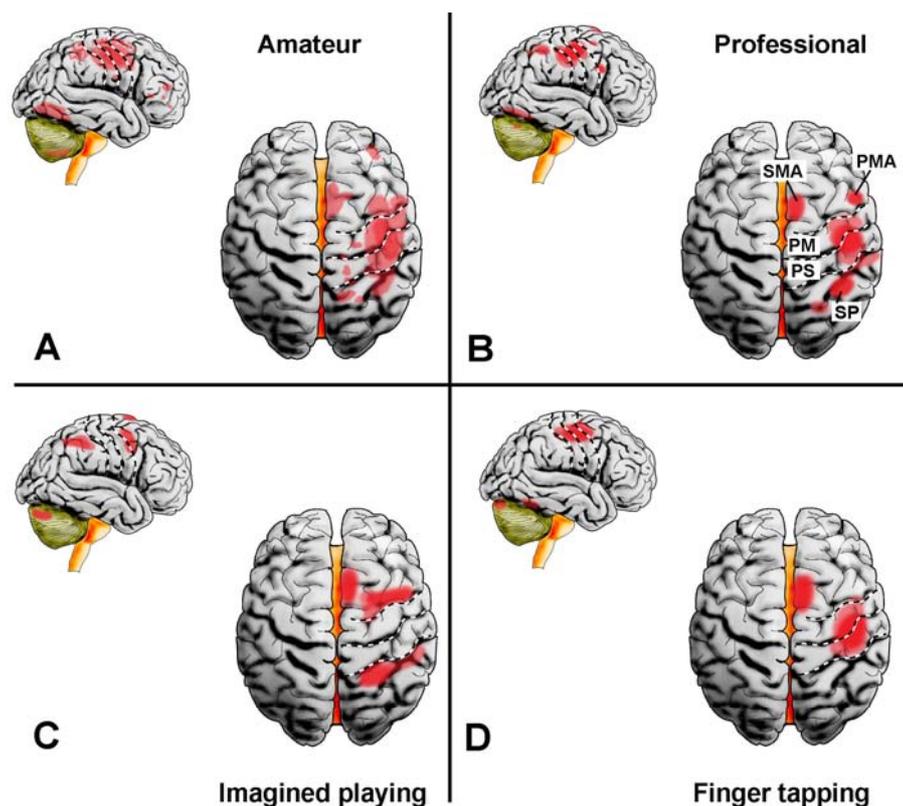


Fig. 3

Figure 3. Patterns of cortical activity visualized using functional MRI **A, B.** A comparison between cortical activity in amateur and professional violinists asked to finger the left hand movements needed to perform 16 bars of a Mozart violin sonata. Both groups show similar patterns of activity, but this is more focused in the professionals. The position of the central sulcus, and the limits of the primary motor and sensory areas are indicated by the dashed lines. The strongest activity straddles this line in a region that represents the sensory and motor representation of the left hand. Activity within the premotor (PMA) and supplementary motor areas (SMA) is indicated. **C,D.** A comparison between cortical activity in a violinist mentally rehearsing a Bach partita (**C**) with activity during a bilateral finger tapping exercise (**D**). Note that during the imagined playing, there is no activity in the primary motor and sensory areas, though there is marked activity in the premotor (PMA), supplementary motor (SMA) and superior parietal (SP) areas. During the finger tapping exercise, the hand region of the primary motor and primary sensory areas are strongly activated.

For copyright reasons these are schematic drawings of images from published papers. The original images can be found in Lotze et al. (2003) (**A,B**) and Langheim et al. (2002) (**C-D**).

through interhemispheric communication (Hund-Georgiadis & von Cramon, 1999). Though such transference has not been observed in all studies and therefore remains controversial, we shall see later that focal dystonia in one hand can quickly appear in the other if it is used to carry out tasks formerly assigned to the dystonic one. If, as has been proposed, this type of dystonia is an effect of overtraining, its transference to the other hand would be consistent

with a bilateral effect of training on the sensory-motor cortex.

Instrumental rehearsal in practice

In the initial stages of learning a new piece, reading through the score may be used to gain a clear idea of the notes and expression marks in the absence of the distraction of the physical challenges of playing. This can take the form of studying the overall structure of the piece and/or a careful examination of single phrases or their component note sequences. Music has its own grammar, and when based on conventional harmonies or chordal progressions, only certain sequences are to be expected. Recognising this should increase the probability of playing the notes accurately at the first attempt and in so doing, establishing the correct motor programme from the outset. Technical exercises of various types, including those based on scales, are designed to inculcate just such motor subroutines. We have already seen that finger movements must be repeated many times to generate the initial increased cortical response that underlies the first stage of motor learning. If several variants are played initially, this will at the very least slow the consolidation of the correct motor sequence, and at worst lead to the firm establishment of an incorrect version that may persist for some time as a learned alternative to the correct one (especially if the incorrect sequence is easier to perform). The importance of the initial stages of learning is borne out by observations of how high level performers actually practice. One study recorded how a pianist set about learning and memorising a movement from Bach's Italian concerto from first seeing the piece, till a performance level of execution was achieved. Different short segments of one awkward eight bar sequence were repeated more than 150 times during the first practice session, and a further 50 times in the second session (Chaffin & Lemieux, 2004). In subsequent practice sessions, it was never singled out for special treatment indicating that the motor sequence had been effectively mastered. This demonstrates the efficacy of this highly focussed approach to motor learning often known as "deliberate practice". Animal studies also suggest that focussed attention plays a significant role in determining the efficacy of motor practice (Schmied et al., 2000). It therefore appears that the pianist had intuitively arrived at a strategy that is consistent with the results of more objective scientific studies.

Mental rehearsal

For many professional musicians, mental rehearsal is an integral part of performance preparation. Its is strongly promoted by some teachers and its use by well known pianists such as Horowitz and Rubenstein is a matter of record. In neurobiological terms, mental rehearsal and preparation can be seen to encompass several distinct elements. First, there is the interpretation of the score in terms of an internal representation of sound (i.e. mentally hearing the music when reading the score). Second, there is the committing of the score to memory, which includes not only the notation on the staff, but also the marks of expression. Playing from memory reduces the cognitive load of performance and allows greater attention to be given to assessment the sound being produced. Only when memorisation has been

achieved does the final stage of using the score to support a virtual rehearsal of the movements required to perform it, become possible. In its most advanced stages, this may even be used to explore various options for expressive interpretation. For this to be possible, the brain must create an internal image not only of the movements but also of the precise effect they will have on the sound. Though they are combined holistically, each of these tasks requires a different set of mental skills, however we will concentrate primarily on the mental rehearsal of playing movements. It assumes a complete familiarity with, and mastery of, the instrument and is therefore an option open only to advanced players (Lotze et al., 2003). This form of physical imagery is not unique to musicians; it is widely used in sports which involve complex stereotyped movements. High jumpers for example, can often be seen mentally practising using minimal or reduced movements before a crucial jump. Perhaps surprisingly, the effectiveness of mental practice in improving aspects of the dynamics of movement, such as the accuracy of a movement trajectory has been verified experimentally (Yaguez et al., 1998). In one study, the effect of mental rehearsal was compared with physical practice of the same simple musical passage on the keyboard (Pascual-Leone, 2001). The subjects practiced mentally (i.e. rehearsing the activity in the absence of any movement or muscle activity) or physically for two hours daily over five days. The effect of this on the representation of the hand in the motor cortex was assessed by comparing the efficacy of transcranial magnetic stimulation¹⁷ in eliciting movement of the trained and untrained hand. Though the section of the primary motor cortex which drives the muscles of the hand remained silent in the group carrying out only mental rehearsal, the size of the areas that were able to activate the muscles moving the fingers increased, while their threshold for activation was reduced. This was accompanied by a demonstrable improvement in the accuracy of motor performance though it was not as great as that achieved through physical practice. However at the end of the study, a single session of physical practice in the mental rehearsal group was sufficient for them to reach parity of performance with the physical rehearsal group. This result is in general agreement with those of other less physiologically rigorous studies which suggest that while mental practice is better than no practice, it is not as good as actual practice (Gabrielsson, 1999). Professional musicians who play a great deal can be prone to overuse injury however, so one advantage of mental practice is that it can be used to refine or improve performance while reducing this risk.

Clearly one source of information missing in mental rehearsal is sensory feedback in the form of touch (exteroception) or of sensation from muscles and tendons (proprioception). The less experienced the player, the more important this feedback will be, however in experienced players in whom the movements of the fingers have become fully automatic, its importance may be reduced. There is also of course a lack of auditory feedback as there is no tangible output from the virtual activity. The effect of its absence on performance accuracy has been investigated in experienced pianists playing on a silent keyboard (Finney & Palmer, 2003).

¹⁷ A method of stimulating the brain through the skull using magnetic fields.

For substantial excerpts of previously learned music (for example pieces by Bach, Beethoven and Rachmaninov) there was no significant difference in error rate between playing with or without sound. In simple sight reading tests however, though the absence of auditory feedback had no effect on performance from the score, it did have a negative effect on the accuracy of the music when it was subsequently repeated from memory.

With the exception of the primary motor and sensory areas, many of the other cortical regions that are normally active during playing are also active during virtual practice (Langheim et al., 2002; Lotze et al., 2003; Meister et al., 2004). Functional imaging studies (the use of brain scans to reveal activity in different regions of the living brain) have revealed activity in premotor and supplementary motor areas which are thought to be involved in the generation of complex motor activity (Fig. 3C-D). The premotor area was active when the physical performance of a melody was silently recreated in the mind, though not when the melody was simply recalled. Perhaps surprisingly, there was no activity in the primary auditory area during these experiments, despite the fact that virtual rehearsal generally requires a vivid mental realisation of the sound associated with the virtual “movements”. This is in contrast to imagining a scene, which does produce activity in visual cortical areas. However, when the rehearsal involved real hand movements, activity was present in the right primary auditory cortex and left auditory association cortex even if the hand was not in contact with the instrument (Lotze et al., 2003). This suggests that some link exists between the primary motor and auditory areas (Bangert & Altenmuller, 2003). The right primary auditory cortex is the main region involved in the perception of pitch, harmony and timbre and its level of activity during silent practice with actual finger movements is greater in the professional musicians than in the amateurs. A link in the opposite direction between the primary auditory and primary motor cortices has also been demonstrated. A study of advanced piano students demonstrated that listening to a piece of keyboard music with which they were already familiar caused involuntary activity in the primary motor cortex even though no contraction of muscles moving the fingers took place (Hauelsen & Knosche, 2001). Activity in the motor cortex occurred in the region controlling a finger just before the note it would have played was sounded and so it mirrored the activity that would have been required for playing. No such response was seen in a control group of similarly experienced singers who were not pianists. This type of connection would undoubtedly support the ability to play by music by ear.

Occupational Focal Dystonia in musicians – a consequence of maladaptive cortical remodelling?

Dystonia refers to abnormal involuntary and uncontrollable muscle contractions that are often seen in the hand, or in muscles of the neck or face. It is said to be focal when it affects only single muscle or small group of muscles. This is generally task specific, particularly affecting activities that have habitually been carried out for prolonged periods as part of the patient's occupation. Occupational focal dystonia is twice as common in men than in women, and most

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typically appears in the fourth decade of life (Hochberg & Hochberg, 2000; Lim et al., 2001; Wynn Parry & Tubiana, 1998) though it is not entirely unknown at an earlier age (Jankovic & Shale, 1989). Among musicians it therefore tends to develop in mid-career in individuals who already have a sound and well established technique. The consequences may not initially be obvious to the listener, and the condition sometimes take years to development fully; however in some cases the dystonia becomes debilitating in a matter of months (Tubiana, 2000). Because dystonia has been widely discussed in recent literature on the health of musicians, they may have an exaggerated impression of its incidence. This appears to be of the order of 1:200-1:500 (Lim et al., 2001) which is about ten times the level seen in the general population (Pullman & Hristova, 2005; Wynn Parry & Tubiana, 1998). Dystonia is most commonly reported among pianists and guitarists, though the hands of other string players, and of woodwind and brass players may also be affected. In addition focal dystonia of the embouchure is seen in some wind players (Frucht et al., 2001).

Symptoms of focal dystonia in musicians

The onset of dystonia is usually gradual and painless. An unaccountable inability to control the hand may start first as a feeling of heaviness in the fingers but become progressively more debilitating. Among keyboard players there is initially a loss of facility in passages that may have been executed without problems for decades (Hochberg & Hochberg, 2000; Tubiana, 2000). In rapid passages, particularly those containing arpeggios, some of the fingers may appear to lag behind the others in an unaccountable way. In string players, difficulties may be experienced with double stopping as well as with passage work, in which a finger or fingers may slow to lift. As the condition progresses the affected fingers often assume a more flexed posture. In pianist it may this may cause the edge of the nail strikes the piano key while string players may find it hard to raise the finger from between the strings. Ultimately the fingers may become so completely curled under the palm that the outer surface of the nail strikes the key instead of the pad (Candia et al., 2002). In other cases the recalcitrant fingers may become involuntarily extended so that they cannot be brought down to touch the key or string. The later stages of dystonia are sometimes characterised by a fierce simultaneous contraction of antagonistic flexor and extensor muscles of the digits that causes fatigue and pain. Interestingly, in patients who play more than one instrument (for example piano and violin), the dystonia may affect the playing of only one. Activities such as typing, which one might think would share many similarities with keyboard playing may, initially at least, remain unaffected (Wynn Parry & Tubiana, 1998). The typical site of the dystonia varies depending on the instrument. Wynn-Parry et al. report that in pianists, it is the right hand that is most frequently dystonic (70%) in which case the most commonly affected fingers are those closest to the little finger. When the left hand is involved, the affected digits tend to be on the other side of the hand. Among guitarists, it is the index and ring fingers of the right hand that are most likely to become dystonic while in violinists, three quarters of cases involve the left hand.

Theories of the origin of dystonia

A full discussion of the theories of the origin of focal dystonia are beyond the scope of this review, but an account of these can be found in (Lim et al., 2001). Some researchers have proposed a strong causal link between focal dystonia and repetitive strain injury (Byl & McKenzie, 2000) however the relationship with injury remains unclear. While some anecdotal evidence has been put forward to support the idea that a variety of injuries may trigger dystonia (Jankovic & Shale, 1989) a lack of objectivity in the way the data was collected, and an absence of any rationale to explain the theory, undermines its credibility. In addition, the average age of onset for overuse injuries among musicians is in the mid-twenties, while for dystonia it is a decade or more later (Tubiana, 2000).

There is a growing belief that focal dystonia is not fundamentally a malfunction of peripheral motor control but that it has its origins in the central nervous system. Studies of the cortex of monkeys and humans with focal dystonia have revealed a change in the organisation in the primary sensory cortex. In monkeys which develop dystonia after being trained to carry out repetitive hand movements to obtain food, there was a marked degradation of the sensory map of the hand. The near simultaneous stimulation of adjacent fingers during tasks which require close attention appears to be a significant factor in these changes. The receptive fields of cortical neurones receiving information from the fingers were observed to enlarge by a factor of ten or twenty. This causes considerable overlap between the cortical representation of different fingers and between the front and back of the hand (Byl & Melnick, 1997). Receptive fields may grow to cover several finger joints. In musicians, an obsessive approach to practising passages of extreme difficulty appears to be related to the development of focal dystonia of the hand or embouchure and may create a similar set of physical conditions to those just described. In both musicians and non-musicians with focal dystonia of the hand, maladaptive changes are also seen in cortical mapping. The finger representations of the dystonic hand are much closer together (Fig. 4), and may either overlap or be in random order (Bara-Jimenez et al., 1998; Byl et al., 2000; Elbert et al., 1998). There is also evidence of a degradation in the mapping of the non-affected hand of dystonic patients, though this is not as marked as that of the affected hand (Elbert et al., 1998). Braille readers who use several fingers to read text also often show a disordered or fused cortical representation of these fingers which is reflected in the representation of the other hand even though it is not used for reading (Sterr et al., 1998). This suggests that the sensory maps on the two sides of the brain are not fully independent, a fact that may help to explain why dystonia sometimes appears quite quickly in the previously non-affected hand when it takes over tasks previously carried out previously by the dystonic one (Lim et al., 2001).

Focal dystonia is of course a disorder of motor control, so if the idea that it is caused by changes in the sensory map is valid, it should theoretically be possible to demonstrate some

reconfiguration of the motor cortex. In patients with focal hand dystonia such changes have not so far been detected in the motor map of the hand, however given what we already know of the organisation of the primary motor cortex, this is perhaps only to be expected. In musicians with embouchure dystonia however, there is some indication of changes in motor cortical organisation (Hirata et al., 2004). There are also disturbances in the organisation of the sensory-motor maps within the basal ganglia (Delmaire et al., 2005). In addition, changes are seen in other motor areas of the brain in dystonic patients, including musicians (Ibanez et al., 1999; Lim et al., 2001; Lim et al., 2004). For example, during the execution of tasks which induce dystonic symptoms, activity in the posterior part of the supplementary motor cortex is reduced below normal levels while that in the primary motor and sensory cortex is increased. One consequence of the intensive training needed to perfect the rapid and continuous finger movements required by instrumentalists, is a reduction in the inhibition normally seen between the primary motor areas on each side of the brain (Nordstrom & Butler, 2002). Paradoxically, the inhibition is thought to be part of a mechanism that allows the individual muscles acting on the fingers to be controlled independently. The reason why it is reduced in normal musicians is unknown but as a similar pattern is seen in dystonic non-musicians this may predispose them to dystonia. It may be another factor underlying the rapid development of dystonia in the non-affected hand when it is used to compensate for the one initially affected.

Treating focal dystonia in musicians

Currently there has been no effective treatment for focal dystonia that significantly and reliably restores the ability to play the instrument at a high level. A number of drug treatments are used routinely to control the symptoms, the major classes being benzodiazepines, anticholinergics and anti-dopaminergics (Hochberg et al., 1990). In addition, the chronic muscle contractions that can develop may be treated by direct injection of Botulinum toxin¹⁸ into them. In musicians in particular, the dosage and site of injection is critical if the muscle activity required for playing is to be preserved. Though this treatment can have a positive effect for some musicians, in only a minority of cases is it sufficiently successful to allow playing of a professional standard to be maintained (Altenmuller, 2003; Schuele et al., 2005). The recent discovery of the changes in cortical mapping that is associated with occupational focal dystonia has suggested new treatments based not on drugs but on sensory and/or motor re-education. Though there is as yet no consensus on the optimum strategy for this approach and it is still uncertain how successful it will prove to be in the long term, a number of preliminary studies have been carried out to investigate its potential benefits.

¹⁸ Botox. This is a bacterial toxin that causes a paralysis that lasts several weeks by blocking the action of motor neurones on the muscles they supply.

There have been only a few studies of therapies directed specifically at musicians, who are one of the most challenging groups in terms of rehabilitation. One of these used an approach called constraint-induced movement therapy (Candia et al., 2002; Candia et al., 2003; Taub et al., 2002) which was originally designed for the rehabilitation of stroke victims. An initial study involved six pianists, two guitarists, two flautists and an oboist all of whom suffered from dystonia of the hand. In each case, the main finger or fingers which were being used to compensate for the dystonic one were immobilised with splints, leaving the dystonic finger to cope on its own. During a period lasting up to a year, the dystonic finger was required to carry out repetitive movements demanding the coordination of several muscles, for an hour or more each day. After an initial 8 day period of intensive training, many (but not all) of the subjects showed signs of improvement as measured on a subjective self assessment scale. However maintaining and augmenting this improvement required that the treatment be continued regularly for many months. Pianists and guitarists who persisted with the training gained the most from this approach and some reached a level close to normality however the wind players derived little or no benefit. In a further study of ten dystonic musicians, a mechanical device composed of two keys was used to provide an objective assessment of the effectiveness of movement-constraint therapy (Candia et al., 2003). Improvements in finger control of key depression were statistically correlated with the degree of restoration in the structure of the somatosensory map of the dystonic hand.

Another approach to reducing dystonic hand movements in musicians is limb immobilization (Priori et al., 2001). Here a splint is used to completely prevent any movement of the wrist and hand on the affected side for a period of 4-5 weeks. Such a long period of immobilization leads to considerable muscle weakening which take several weeks to recover from, but this approach was reported to produce considerable long term improvement in four of the seven musicians who took part. This treatment is clearly one that merits further investigation with a larger sample of dystonic patients.

Concluding remarks

It is in the nature of musical performance, that succeeding generations push the levels of virtuosity to ever greater heights. This inevitably reveals the limits of the motor system both from an anatomical and a physiological point of view. By re-assessing the anatomy of the muscles and tendons of the hand, we can begin to appreciate that variations in anatomy between individuals will have a significant effect on the possible fingerings which can be used to play certain passages. The combination of functional fMRI with its high spatial resolution, with magneto encephalography, which provides excellent temporal resolution, has made investigation of the effects of training on cortical activity patterns a realistic proposition. As we have seen, by comparing instrumentalists of a professional standard with amateurs and with non-musicians, it has been possible with these techniques to observe the effects of hand

training on activity patterns within the regions of the cortex devoted to motor control. We have concerned ourselves here primarily with the motor system, but the same methods have been used to study the somatosensory system and have revealed changes in the representation of the hand within the primary sensory cortex of non-dystonic instrumentalists (Elbert et al., 1995; Hashimoto et al., 2004). As one might expect, brain imaging techniques have also been applied extensively to studies of auditory processing of both music and sound in musicians, and in those with impairments in musical processing (Deutsch, 1999; Peretz & Zatorre, 2003). Many of factors that make musicians such excellent subjects for studies of motor control apply equally to these studies of sensory processing. Indeed among human subjects who lack sensory, cognitive or motor deficits, they are one of the most interesting groups with specialist skills in which to study patterns of brain activation.

References

- Allieu, Y., Hamitouche, K., Roux, J.L. and Beaton, Y.** (1998), 'Unique surgical conditions', in Winspur, I. and Wynn Parry, C.B. (eds.), *The Musicians Hand: a clinical guide*, London, Martin Dunitz.
- Altenmuller, E.** (2003), 'Focal dystonia: advances in brain imaging and understanding of fine motor control in musicians', *Hand Clin*, 19, 3, 523-38, xi.
- Amunts, K., Schlaug, G., Jancke, L., Steinmetz, H., Schleicher, A., Dabringhaus, A. and Zilles, K.** (1997), 'Motor Cortex and Hand Motor Skills: Structural Compliance in the Human Brain.' *Hum Brain Mapp*, 5, 206-215.
- Amunts, K., Schlaug, G., Schleicher, A., Steinmetz, H., Dabringhaus, A., Roland, P.E. and Zilles, K.** (1996), 'Asymmetry in the human motor cortex and handedness', *Neuroimage*, 4, 3 Pt 1, 216-22.
- Baker, D.S., Gaul, J.S., Jr., Williams, V.K. and Graves, M.** (1981), 'The little finger superficialis--clinical investigation of its anatomic and functional shortcomings', *J Hand Surg [Am]*, 6, 4, 374-8.
- Bangert, M. and Altenmuller, E.O.** (2003), 'Mapping perception to action in piano practice: a longitudinal DC-EEG study', *BMC Neurosci*, 4, 1, 26.
- Bara-Jimenez, W., Catalan, M.J., Hallett, M. and Gerloff, C.** (1998), 'Abnormal somatosensory homunculus in dystonia of the hand', *Ann Neurol*, 44, 5, 828-31.
- Beauchamp, R.** (2003a), 'Curved fingers - and tension', *Music and Health website*, <http://www.musicandhealth.co.uk/tension.html>.
- Beauchamp, R.** (2003b), 'Examples of passages that may cause problems due to tendon linkages or absences', *Music and Health website*, <http://www.musicandhealth.co.uk/linkages.htm>.
- Beauchamp, R.** (2003c), 'Our Anatomical Differences', *Music and Health website*, <http://www.musicandhealth.co.uk/differences.html>.
- Bergman, R.A., Afifi, A.K. and Miyauchi, R.** (2004), 'Illustrated Encyclopedia of Human Anatomic Variation', <http://www.vh.org/adult/provider/anatomy/AnatomicVariants/AnatomyHP.html>.
- Brown, S.** (2000), 'Promoting a healthy keyboard technique', in Tubiana, R. and Amadio, P.C. (eds.), *Medical Problems of the Instrumental Musician*, London, Martin Dunitz.
- Byl, N.N. and McKenzie, A.** (2000), 'Treatment effectiveness for patients with a history of repetitive hand use and focal hand dystonia: a planned, prospective follow-up study', *J Hand Ther*, 13, 4, 289-301.
- Byl, N.N., McKenzie, A. and Nagarajan, S.S.** (2000), 'Differences in somatosensory hand organization in a healthy flutist and a flutist with focal hand dystonia: a case report', *J Hand Ther*, 13, 4, 302-9.
- Byl, N.N. and Melnick, M.** (1997), 'The neural consequences of repetition: clinical implications of a learning hypothesis', *J Hand Ther*, 10, 2, 160-74.

- Candia, V., Schafer, T., Taub, E., Rau, H., Altenmuller, E., Rockstroh, B. and Elbert, T.** (2002), 'Sensory motor retuning: a behavioral treatment for focal hand dystonia of pianists and guitarists', *Arch Phys Med Rehabil*, 83, 10, 1342-8.
- Candia, V., Wienbruch, C., Elbert, T., Rockstroh, B. and Ray, W.** (2003), 'Effective behavioral treatment of focal hand dystonia in musicians alters somatosensory cortical organization', *Proc Natl Acad Sci U S A*, 100, 13, 7942-6.
- Chaffin, R. and Lemieux, A.F.** (2004), 'General perspectives on achieving musical excellence', in Williamon, A. (ed.), *Musical Excellence: strategies and techniques to enhance performance*, Oxford, Oxford University Press.
- Delmaire, C., Krainik, A., Tezenas du Montcel, S., Gerardin, E., Meunier, S., Mangin, J.F., Sangla, S., Garnero, L., Vidailhet, M. and Lehericy, S.** (2005), 'Disorganized somatotopy in the putamen of patients with focal hand dystonia', *Neurology*, 64, 8, 1391-6.
- Deutsch, D.** (1999), *The Psychology of Music* (2nd Edition), San Diego, Academic Press.
- Elbert, T., Candia, V., Altenmuller, E., Rau, H., Sterr, A., Rockstroh, B., Pantev, C. and Taub, E.** (1998), 'Alteration of digital representations in somatosensory cortex in focal hand dystonia', *Neuroreport*, 9, 16, 3571-5.
- Elbert, T., Pantev, C., Wienbruch, C., Rockstroh, B. and Taub, E.** (1995), 'Increased cortical representation of the fingers of the left hand in string players', *Science*, 270, 5234, 305-7.
- Finney, S.A. and Palmer, C.** (2003), 'Auditory feedback and memory for music performance: sound evidence for an encoding effect', *Mem Cognit*, 31, 1, 51-64.
- Frucht, S.J., Fahn, S., Greene, P.E., O'Brien, C., Gelb, M., Truong, D.D., Welsh, J., Factor, S. and Ford, B.** (2001), 'The natural history of embouchure dystonia', *Mov Disord*, 16, 5, 899-906.
- Futami, T., Shinoda, Y. and Yokota, J.** (1979), 'Spinal axon collaterals of corticospinal neurons identified by intracellular injection of horseradish peroxidase', *Brain Res*, 164, 279-84.
- Gabrielsson, A.** (1999), 'The Performance of Music', in Deutsch, D. (ed.), *The Psychology of Music* (2nd Edition), San Diego, Academic Press.
- Gaser, C. and Schlaug, G.** (2003), 'Brain structures differ between musicians and non-musicians', *J Neurosci*, 23, 27, 9240-5.
- Graziano, M.S., Taylor, C.S., Moore, T. and Cooke, D.F.** (2002), 'The cortical control of movement revisited', *Neuron*, 36, 3, 349-62.
- Hashimoto, I., Suzuki, A., Kimura, T., Iguchi, Y., Tanosaki, M., Takino, R., Haruta, Y. and Taira, M.** (2004), 'Is there training-dependent reorganization of digit representations in area 3b of string players?' *Clin Neurophysiol*, 115, 2, 435-47.
- Haslinger, B., Erhard, P., Altenmuller, E., Hennenlotter, A., Schwaiger, M., Graf von Einsiedel, H., Rummeny, E., Conrad, B. and Ceballos-Baumann, A.O.** (2004), 'Reduced recruitment of motor association areas during bimanual coordination in concert pianists', *Hum Brain Mapp*, 22, 3, 206-15.
- Hauelsen, J. and Knosche, T.R.** (2001), 'Involuntary motor activity in pianists evoked by music perception', *J Cogn Neurosci*, 13, 6, 786-92.
- Hirata, Y., Schulz, M., Altenmuller, E., Elbert, T. and Pantev, C.** (2004), 'Sensory mapping of lip representation in brass musicians with embouchure dystonia', *Neuroreport*, 15, 5, 815-8.
- Hochberg, F.H., Harris, S.U. and Blatter, T.R.** (1990), 'Occupational hand cramps: professional disorders of motor control', *Hand Clin*, 6, 3, 417-28.
- Hochberg, F.H. and Hochberg, N.S.** (2000), 'Occupational Cramps/Focal Dystonias', in Tubiana, R. and Amadio, P.C. (eds.), *Medical Problems of the Instrumental Musician*, London, Martin Dunitz.
- Hund-Georgiadis, M. and von Cramon, D.Y.** (1999), 'Motor-learning-related changes in piano players and non-musicians revealed by functional magnetic-resonance signals', *Exp Brain Res*, 125, 4, 417-25.
- Hutchinson, S., Lee, L.H., Gaab, N. and Schlaug, G.** (2003), 'Cerebellar volume of musicians', *Cereb Cortex*, 13, 9, 943-9.
- Ibanez, V., Sadato, N., Karp, B., Deiber, M.P. and Hallett, M.** (1999), 'Deficient activation of the motor cortical network in patients with writer's cramp', *Neurology*, 53, 1, 96-105.
- Jancke, L., Schlaug, G. and Steinmetz, H.** (1997), 'Hand skill asymmetry in professional musicians', *Brain Cogn*, 34, 3, 424-32.

- Jankovic, J. and Shale, H.** (1989), 'Dystonia in musicians', *Semin Neurol*, 9, 2, 131-5.
- Kandel, E.R., Schwartz, J.H. and Jessell, T.M.** (2000), *Principles of neural science* (4th Edition), New York, McGraw-Hill, Health Professions Division.
- Karni, A., Meyer, G., Jezzard, P., Adams, M.M., Turner, R. and Ungerleider, L.G.** (1995), 'Functional MRI evidence for adult motor cortex plasticity during motor skill learning', *Nature*, 377, 6545, 155-8.
- Karni, A., Meyer, G., Rey-Hipolito, C., Jezzard, P., Adams, M.M., Turner, R. and Ungerleider, L.G.** (1998), 'The acquisition of skilled motor performance: fast and slow experience-driven changes in primary motor cortex', *Proc Natl Acad Sci U S A*, 95, 3, 861-8.
- Kleim, J.A., Hogg, T.M., VandenBerg, P.M., Cooper, N.R., Bruneau, R. and Remple, M.** (2004), 'Cortical synaptogenesis and motor map reorganization occur during late, but not early, phase of motor skill learning', *J Neurosci*, 24, 3, 628-33.
- Kuang, R.Z. and Kalil, K.** (1990), 'Branching patterns of corticospinal axon arbors in the rodent', *J Comp Neurol*, 292, 4, 585-98.
- Langheim, F.J., Callicott, J.H., Mattay, V.S., Duyn, J.H. and Weinberger, D.R.** (2002), 'Cortical systems associated with covert music rehearsal', *Neuroimage*, 16, 4, 901-8.
- Lee, D.J., Chen, Y. and Schlaug, G.** (2003), 'Corpus callosum: musician and gender effects', *Neuroreport*, 14, 2, 205-9.
- Leijnse, J.N., Bonte, J.E., Landsmeer, J.M., Kalker, J.J., Van der Meulen, J.C. and Snijders, C.J.** (1992), 'Biomechanics of the finger with anatomical restrictions--the significance for the exercising hand of the musician', *J Biomech*, 25, 11, 1253-64.
- Leijnse, J.N., Snijders, C.J., Bonte, J.E., Landsmeer, J.M., Kalker, J.J., Van der Meulen, J.C., Sonneveld, G.J. and Hovius, S.E.** (1993), 'The hand of the musician: the kinematics of the bidigital finger system with anatomical restrictions', *J Biomech*, 26, 10, 1169-79.
- Leijnse, J.N., Walbeehm, E.T., Sonneveld, G.J., Hovius, S.E. and Kauer, J.M.** (1997), 'Connections between the tendons of the musculus flexor digitorum profundus involving the synovial sheaths in the carpal tunnel', *Acta Anat (Basel)*, 160, 2, 112-22.
- Lim, V.K., Altenmuller, E. and Bradshaw, J.L.** (2001), 'Focal dystonia: current theories', *Hum Mov Sci*, 20, 6, 875-914.
- Lim, V.K., Bradshaw, J.L., Nicholls, M.E. and Altenmuller, E.** (2004), 'Abnormal sensorimotor processing in pianists with focal dystonia', *Adv Neurol*, 94, 267-73.
- Lotze, M., Scheler, G., Tan, H.R., Braun, C. and Birbaumer, N.** (2003), 'The musician's brain: functional imaging of amateurs and professionals during performance and imagery', *Neuroimage*, 20, 3, 1817-29.
- Mehta, H.J. and Gardner, W.U.** (1961), 'A study of lumbrical muscles in the human hand', *Am J Anat*, 109, 227-38.
- Meister, I.G., Krings, T., Foltys, H., Boroojerdi, B., Muller, M., Topper, R. and Thron, A.** (2004), 'Playing piano in the mind--an fMRI study on music imagery and performance in pianists', *Cogn Brain Res*, 19, 3, 219-28.
- Miller, G., Peck, F., Brain, A. and Watson, S.** (2003), 'Musculotendinous anomalies in musician and nonmusician hands', *Plast Reconstr Surg*, 112, 7, 1815-22; discussion 1823-4.
- Nordstrom, M.A. and Butler, S.L.** (2002), 'Reduced intracortical inhibition and facilitation of corticospinal neurons in musicians', *Exp Brain Res*, 144, 3, 336-42.
- Parlitz, D., Peschel, T. and Altenmuller, E.** (1998), 'Assessment of dynamic finger forces in pianists: effects of training and expertise', *J Biomech*, 31, 11, 1063-7.
- Parsons, L.M.** (2003), 'Rethinking the lesser brain.' *Sci Am*, 289, 2, 40-47.
- Pascual-Leone, A.** (2001), 'The brain that plays music and is changed by it', *Ann N Y Acad Sci*, 930, 315-29.
- Penfield, W. and Rasmussen, T.** (1950), *The cerebral cortex of man; a clinical study of localization of function*, New York, Macmillan.
- Peretz, I. and Zatorre, R.J.** (2003), *The cognitive neuroscience of music*, Oxford ; New York, Oxford University Press.
- Perkins, R.E. and Hast, M.H.** (1993), 'Common Variations in Muscles and Tendons of the Human Hand', *Clin Anat*, 6, 226-231.
- Priori, A., Pesenti, A., Cappellari, A., Scarlato, G. and Barbieri, S.** (2001), 'Limb immobilization for the treatment of focal occupational dystonia', *Neurology*, 57, 3, 405-9.

- Pullman, S.L. and Hristova, A.H.** (2005), 'Musician's dystonia', *Neurology*, 64, 2, 186-7.
- Reilly, K.T., Nordstrom, M.A. and Schieber, M.H.** (2004), 'Short-term synchronization between motor units in different functional subdivisions of the human flexor digitorum profundus muscle', *J Neurophysiol*, 92, 2, 734-42.
- Ridding, M.C., Brouwer, B. and Nordstrom, M.A.** (2000), 'Reduced interhemispheric inhibition in musicians', *Exp Brain Res*, 133, 2, 249-53.
- Sanes, J.N. and Schieber, M.H.** (2001), 'Orderly somatotopy in primary motor cortex: does it exist?' *Neuroimage*, 13, 6 Pt 1, 968-74.
- Schieber, M.H. and Hibbard, L.S.** (1993), 'How somatotopic is the motor cortex hand area?' *Science*, 261, 5120, 489-92.
- Schlaug, G.** (2001), 'The brain of musicians. A model for functional and structural adaptation', *Ann N Y Acad Sci*, 930, 281-99.
- Schlaug, G., Jancke, L., Huang, Y. and Steinmetz, H.** (1995), 'In vivo evidence of structural brain asymmetry in musicians', *Science*, 267, 5198, 699-701.
- Schmied, A., Ivarsson, C. and Fetz, E.E.** (1993), 'Short-term synchronization of motor units in human extensor digitorum communis muscle: relation to contractile properties and voluntary control', *Exp Brain Res*, 97, 1, 159-72.
- Schmied, A., Pagni, S., Sturm, H. and Vedel, J.P.** (2000), 'Selective enhancement of motoneurone short-term synchrony during an attention-demanding task', *Exp Brain Res*, 133, 3, 377-90.
- Schuele, S., Jabusch, H.C., Lederman, R.J. and Altenmuller, E.** (2005), 'Botulinum toxin injections in the treatment of musician's dystonia', *Neurology*, 64, 2, 341-3.
- Shinoda, Y., Yamaguchi, T. and Futami, T.** (1986), 'Multiple axon collaterals of single corticospinal axons in the cat spinal cord', *J Neurophysiol*, 55, 3, 425-48.
- Sloboda, J.A., Davidson, J.W., Howe, D.G. and Moore, D.G.** (1996), 'The role of practice in the development of performing musicians.' *Brit J Psychol*, 87, 2, 287-309.
- Sterr, A., Muller, M.M., Elbert, T., Rockstroh, B., Pantev, C. and Taub, E.** (1998), 'Changed perceptions in Braille readers', *Nature*, 391, 6663, 134-5.
- Taub, E., Uswatte, G. and Elbert, T.** (2002), 'New treatments in neurorehabilitation founded on basic research', *Nat Rev Neurosci*, 3, 3, 228-36.
- Tubiana, R.** (2000), 'Musician's Focal Dystonia', in Tubiana, R. and Amadio, P.C. (eds.), *Medical Problems of the Instrumental Musician*, London, Martin Dunitz.
- Wynn Parry, C.B. and Tubiana, R.** (1998), 'Dystonia', in Winspur, I. and Wynn Parry, C.B. (eds.), *The Musicians Hand: a clinical guide*, London, Martin Dunitz.
- Yaguez, L., Nagel, D., Hoffman, H., Canavan, A.G., Wist, E. and Homberg, V.** (1998), 'A mental route to motor learning: improving trajectory kinematics through imagery training', *Behav Brain Res*, 90, 1, 95-106.
- Zeuner, K.E., Bara-Jimenez, W., Noguchi, P.S., Goldstein, S.R., Dambrosia, J.M. and Hallett, M.** (2002), 'Sensory training for patients with focal hand dystonia', *Ann Neurol*, 51, 5, 593-8.