From Laetoli to Carnegie:
Evolution of the Brain and Hands as Prerequisites of Music Performance in Light of Music Physiology and Neurobiology

Eckart O. Altenmüller

Dedicated to my brother Hartwig, the passionate Egyptologist and enthusiasistic musician

ZUSAMMENFASSUNG

Professionelles Musizieren in heutiger Zeit stellt wohl die höchsten Anforderungen an die menschliche Feinmotorik. Gegenstand der Arbeit ist die Frage, wann derartige hoch spezialisierte Handfertigkeiten entwickelt wurden. Das Studium der Instrumente und der Instrumentaltechnik aus prähistorischer und historischer Zeit mag zur Klärung dieser Frage beitragen. Die Hirnstruktur und die Anatomie des Handskelettes des frühen Homo sapiens (archaius) legen die Vermutung nahe, dass die Voraussetzungen für den differenzierten Gebrauch der menschlichen Hand bereits hunderttausende von Jahren vor dem nachweislich frühesten Auftreten von Musikinstrumenten gegeben waren. Unsicher bleibt, welchen Grad der Komplexität unabhängige Fingerbewegungen zum Beispiel beim Flötenspiel in prähistorischer Zeit erreichte. In historischer Zeit ist eindeutig eine Zunahme der Anforderungen an die Handgeschicklichkeit zu konstatieren, die einerseits mit der zunehmenden Spezialisierung der Berufsmusiker und andererseits mit der Verfeinerung von Musikinstrumenten einher geht. Neurobiologische Befunde zeigen, dass das Zentralnervensystem auf die intensive Übung mit Anpassungsvorgängen reagiert, die sich in einer strukturellen Vergrößerung besonders stark beanspruchter Hirnregionen und in einer funktionellen Veränderung der an manuellen Fertigkeiten beteiligten neuronalen Netzwerke niederschlägt. Diese als „funktionsgesteuerte Plastizität“ des Nervensystems bezeichnete Fähigkeit zur Anpassung gehört mit größter Wahrscheinlichkeit zur Grundausstattung von Homo sapiens schon vor dem Auftreten der großen Kulturleistungen. Ab dem 19. Jahrhundert treten mit der „fokalen Dystonie“ berufsspezifische Erkrankungen in Zusammenhang mit starker Beanspruchung am Instrument auf. Die Erkrankung ist durch den Verlust der feinmotorischen Kontrolle gekennzeichnet und geht mit einer Vergröberung der Handrepräsentation im Zentralnervensystem einher. Sie kann damit als ein Endpunkt der Entwicklungsmöglichkeiten von Handfertigkeiten bei Homo sapiens verstanden werden. Die „Evolution“ von Handfertigkeiten bei Musikern ist nach unserer Auffassung daher auf einen Prozess der Anpassung des Zentralnervensystems an zu-nehmende Spezialisierung zurückzuführen und nicht auf eine Veränderung genetischer Information durch Selektion.

1. INTRODUCTION: THE DIALOGUE BETWEEN PHYSIOLOGY AND ARCHAEOLOGY OF MUSIC

"The most intricately and perfectly co-ordinated of all voluntary movements in the animal kingdom are those of the human hand and fingers, and perhaps in no other human activity do memory, complex integration, and muscular co-ordination surpass the achievements of the skilled pianist" (Homer W. Smith, 1953).

What does the physiology of music have to do with music archaeology? What kind of connection links these two seemingly different fields? Music physiologists are interested in the (neuro)biological foundations of music-making and music perception. Their fields of research comprise sensorimotor aspects of music-making and motor learning. By determining the uppermost limits of these uniquely developed skills, specific to humans, by describing the rules of sensorimotor learning and mislearning, music physiologists gain insights into the wonderful and enigmatic machinery of our mind and body. Thus, the understanding of humans' capacity to perform music serves as a window to a general understanding of central nervous sensorimotor processing.

For thousands of years, it has been through the hands of musicians mastering their instruments that humans have communicated the language of emotions, music. In modern times we are fascinated by the precise execution of very fast, and in many instances, extremely complex movement patterns, characterising the skills of professional musicians when performing as virtuosos. But when did this faculty develop? Can we infer something about the improvement of human fine motor skills by studying the development of their probably most demanding tools, their musical instruments? Can music archaeologists provide an answer to questions concerning human evolution? Or, looking at the problem from another perspective: if a time machine had enough place for a Steinway Grand Piano and an expert piano teacher, could an inhabitant of Ancient Egypt, given that he is properly instructed during childhood and adolescence, learn to perform the Liszt B minor piano sonata?

2. THE PREREQUISITES: A SHORT REVIEW OF THE ANATOMY OF THE HANDS AND BRAIN IN LIGHT OF THE EVOLUTION OF MANUAL SKILLS

It is in the human hand that we have the consummation of all perfection as an instrument (Charles Bell, 1840)

The big revolution arose with the capacity of hominids not only to use tools, but also to fabricate tools (M. Wiesendanger, 1999)

The first milestone in the development of manual skills was bipedalism, freeing the hands from locomotion for dextrous behaviour. The emergence of the upright gait of early hominids is documented by the sensational discovery of footprints of *Australopithecus Afarensis* in the Laetoli river beds of Tanzania in 1978. The footprints, dating back about 3.6 million years and investigated by Leakey and Hay[1] belonged to two adults and a child walking at the same stride as if holding hands with one another. The weight distribution on the feet is similar to that of modern man. But most remarkable is the fact that the big toe is parallel to the other toes, suggesting that these early hominids relied exclusively on upright bipedal locomotion and had lost their ability to grasp branches of trees with their feet like their ancestors. This notion is supported by the discovery of a knee joint of *Australopithecus* found earlier in Hadar, Ethiopia, showing equally the biomechanical characteristics of bipedalism.[2] With respect to the anatomy of the hands, *Australopithecus* was able to execute the precision grip, pinching an object between an opposable thumb and the index finger. However, according to Marzke,[3] *Australopithecus* was unable to bring the thumb tip all the way across the hand to the fourth and fifth finger, a movement pattern known as 'ulnar opposition'. Ulnar opposition seems to be unique to modern humans and has the advantage 1) of facilitating the manipulation of small objects between the fingers without contact with the palm and 2) of using all five fingers in the fine control of small objects.[4] The increased movement range of the thumb is based on a relatively subtle modification of the saddle-shaped carpo-metacarpal joint at the base of the thumb. But the anatomical findings do not tell us how the hands were used. Skilled movements like handling a small piece of fruit using ulnar opposition does not only rely on anatomical properties, but more critically on central nervous processing. In contrast to the power grip, requiring a relatively uniform synergy of contracting flexor muscles, the precision grip needs a highly elaborate and fractionated pattern of muscle activity, particularly during movement of the digits into the precision grip posture. The grip itself is associated with a very variable pattern of muscular co-contraction of many different, partly antagonist muscles with different levels of activity organised into a specific pattern.[5] However, it is not only the programming of muscular activity that poses a challenge. Processing of three-dimensional body coordinates and object coordinates, knowledge about the mechanical properties of the handled objects, precision of motor programming and rapid reciprocal visual, somatosensory and motor information transfer are necessary. Furthermore, mental representations of all these properties have to be maintained in procedural memory. It is questionable whether the 400–530 ccm size brains of an *Australopithecine* were sufficient for such complex central nervous processing.

It is clear that although the *Australopithecine* hand could have used tools the brain was not large enough to fabricate tools. It took more than a million of years until *Homo habilis* and the 'Oldo-

1 Leakey and Hay 1979.
2 Johanson and Taieb 1976.
3 Marzke 1997.
4 For a review on this topic see the excellent chapter 'Dawn' in F. Wilson, 1999.
5 Hepp-Reymond et al. 1996.

wan' industrial complex arose. The earliest direct evidence of hominid technology dates back 2.5 million years in the Ethiopian rift valley comprising sharp-edged slivers and lumps of stone, hammer stones and anvils and bones with hammer marks and cut marks. The hand of *Homo habilis* resembles that of modern humans and his brain was with 600 to 800 ccm, significantly larger than that of earlier or contemporary *Australopithecines*. Cranial endocasts show that its left hemisphere leaves an impression of Broca's Area on the skull, suggesting that hemispheric specialisation arose at this time.[6] Handedness with a right-hand preference for skilled behaviour started to develop at these times. An analysis of stone tools revealed that about 56% of the artefacts were produced with precise strokes of the right hand, the left hand gripping the stone core.[7] But as Wiesendanger points out, "the more than a million years needed, after the hands were already freed, for the emergence of tool production, is an astoundingly long time-span and certainly not a revolution".[8] The slow pace of progress continued. Oldowan technology was maintained over a million years. The subsequent Acheulean industry was manufactured by *Homo erectus* and *Homo Heidelbergiensis*, who were mostly right-handed hominids with increasingly larger brains starting from about 850 ccm 1.5 million years ago to 1200 ccm one million years later. The stone tools of the Acheulean period are not only characterised by their refinement, increased aesthetic value and advanced efficiency, but also by their purpose guided specificity reflecting more complex cognitive abilities.

Technological and cultural evolution accelerated 300,000 years ago. Palaeoanthropologists speculate that this acceleration was due to larger home-ranges, regional interaction and exchange networks that could have facilitated long distance population movements. Furthermore the increasingly variable, severe and risky environments of glacial and interglacial cycles as well as more short-term climatic events might have challenged the Neanderthals, late Archaic humans and finally anatomical modern humans to invent and develop new means of survival under difficult circumstances.[9]

About 130,000 years ago, modern humans appeared first in central Africa, later in the Middle East, Europe and Asia. Their brain size was with about 1400 to 1500 ccm within the range of present humans. Endocasts of these skulls reveal exactly the same patterns of 'gyri' and 'sulci' as found presently.[10] This suggests that the neural bases of cognitive processing and especially of 'modern' skilled behaviour was present long before documentation of elaborate sensorimotor problem solving is evident. About 100,000 years later, this evidence arises, interestingly mainly in the context of the arts. Musical instruments dating back about 35,000 years, and the beautiful ivory carvings from Geissenklösterle and Vogelherd (about 30,000 years old)[11] are amongst the first evidence of highly elaborate sensorimotor conceptualisation of mental representations of humans outer and inner worlds. The common roots of all these kinds of hand dexterity and of music-making were the establishment and maintenance of social bonds, the need to communicate.

In conclusion, it was with the appearance 130,000 years ago of modern brain size, hand anatomy and of music and grammatical language as two ways of organising social groups – emotionally and rationally, that the pace not of bodily, but rather of cognitive evolution sped up exponentially. As Ambrose points out, it is probable that "these changes were increasingly autocatalytic, driven by language and by cultural systems of knowledge and understanding of nature and society. A mere 12,000 years separate the first bow and arrow from the international space station".[12] Musicians are more traditional: to arrive after 40,000 years from a Bone flute to a Boehm flute may be classified as a comparably insignificant step. However, the nature of music may well be the conservative part of our emotional systems. Music may symbolise more archaic needs, coming from the ages of early humanoids to us.

3. THE PARALLELS: A QUICK VIEW OF THE COMPARATIVE PHYSIOLOGY AND HUMAN ONTOGENY OF SKILLED BEHAVIOUR

It would be difficult to name any movement that is possible in the human hand which is not equally possible in the hand of the old world monkeys …
(Wood Jones, 1920)

In the preceding paragraph, it is argued that the anatomical bases of skilled behaviour were developed long before the first documentation of the extraordinary dexterity of *Homo sapiens* was recorded. A quick overview of the manual skills of non-human primates supports the notion of the early emergence of the potential for skilled hand

6 Ambrose 2001.
7 Grüsser 1988.
8 Wiesendanger 1999, 3.
9 Ambrose 2001.
10 Bräuer 1994.
11 Hahn 1987.
12 Ambrose 2001, 1752.

movement. Marianne Christel[13] used high speed films to compare the hand movements of Bonobos (*Pan paniscus*), which are closely related to chimpanzees, and humans while reaching and grasping small objects. Both species were similarly successful in this task. The Bonobos required considerably less time for the visually-guided ballistic reaching movement. In contrast, for grasping and picking up the small objects, mainly guided by sensorimotor systems, they needed a much longer time compared to humans. In general, Bonobos were able to execute a tip-to-tip precision grip, but used another movement strategy. They did not anticipate the grip movement during the reaching phase by adjusting their finger position in advance, and therefore had to compensate for their quick approach with a longer manipulation of the object. Transferring this observation into the frame of evolutionary biology, it can be argued that it is not the anatomy of motor systems and hands, but rather brain development allowing for anticipation and conceptualisation of actions, which was the important step in evolution.

With respect to Haeckels famous sentence of "ontogeny as a repetition of phylogeny",[14] it might be well worth a closer look at the maturation of fine motor skills in human infants. The neurobiological basis of human dexterity is generally attributed to the corticospinal tract, a neural pathway originating from the primary motor cortex and projecting to the spinal cord.[15] Lesions of this motor pathway lead to the loss of dexterity of the fingers. The individual maturation of the corticospinal tract in humans can be investigated by assessing the central nervous conduction time from the motor cortex to the spinal column. One elegant non-invasive method is the stimulation of cortical neurones through the application of strong magnetic fields on the surface of the skull. With this transcranial magnetic stimulation method it has been shown that the adult limit of the central motor conduction velocity is reached between the ages of 3 to 4 years.[16] We must take into account that the maturation of structures as exemplified here with the corticospinal tract is only one amongst other factors determining the acquisition of skilled independent finger movement. Motor skills in humans continue to improve long after the age of 4 years, during childhood and puberty. The full extent of fine motor capabilities are reached in the years of early adulthood around age 20.[17] In summary, primate studies and developmental neurology provide converging evidence that the bodily prerequisites of the skilled use of the hand are developed at an early stage of both phylogeny and ontogeny. The development of the full wealth of dextrous behaviour in humans may be more associated with prolonged functional changes of brain networks involved in planning, visual and sensorimotor integration, establishment of procedural memory, guidance of attention and conceptualisation of inner images.

4. MUSIC: THE EARLY TIMES

Tief ist der Brunnen der Vergangenheit. Sollte man ihn nicht unergründlich nennen?
(First sentence from "Joseph und seine Brüder". Thomas Mann, 1933)

In 1995, Drago Kunej and Ivan Turk found a flute-like perforated thighbone of a young cave bear at the Divje Babe I cave site in Slovenia. The finding originates from the final phase of the middle Paleolithic period, about 35,000 to 50,000 years ago. Following the arguments of Kunej and Turk,[18] it seems to represent the oldest bone flute preserved up until now. It is beyond the scope of this paper to go into the discussion whether the finding is a flute or just a bone pierced by a carnivore in an abnormal way.[19] For the questions addressed in this paper, the fingering table of the reconstructed Divje Babe flute is more interesting, demonstrating that complex fingerings could have been used on the instrument to obtain the full range of scales. One of the particularly demanding movement patterns presented in the tables is the execution of so-called 'forks', the need to move fingers other than the thumb synchronously in opposite directions when playing two notes in a sequence. An example is the extension of the index and ring finger and synchronous flexion of the middle finger (Fig. 1). In principal, these fingering tables are transferable to other bone flutes with three or more holes, undoubtedly identified as musical instruments dating from the upper Paleolithic period, around 30,000 years B.C.[20]

Clearly, these kind of forked finger movements were not common tasks in ancient hunter-gatherer societies. Even today, about 2% of people are unable to properly execute synchronous antagonists movements of adjacent fingers.[21]

13 Christel 1998.
14 Haeckel 1866, 165.
15 Wiesendanger 1981.
16 Armand et al. 1996.
17 Rutenfranz and Hettinger 1959.
18 Kunej and Turk 2000.
19 A review on this topic is given in Kunej and Turk 2000; see also the papers of Nowell and Chase, d'Errico, Fink, this volume.
20 For a review see Hein and Hahn 1998; see also the paper of Münzel/Seeberger/Hein, this volume.
21 Geoffrey Walsh, personal communication and Altenmüller, Walsh and Jabusch, 2001 submitted.

In daily life, similar complex hand movements may occur occasionally. Turning a piece of fruit around in one hand, requires at least three fingers to be moved in a co-ordinated manner with alternating flexion and extension of two adjacent fingers.[22] However, the forked-type movement in flute playing is more complex, since it necessarily includes the use of the fourth finger in both directions, synchronously as well as in antiphase with the middle or the index finger. To our knowledge, no other manipulation besides flute playing could have required such a movement pattern.

Were these movements necessarily executed by the musicians of this time? This is an as yet unsolved and probably unsolvable question. Kunej and Turk admit that "even today with many folk instruments, many players do not exploit all the theoretical and practical sound possibilities of instruments, but restrict themselves to a relatively narrow tonal range that is entirely sufficient for them. Thus the tonal possibilities of an instrument in and of themselves can in no way determine its method of use".[23] Further uncertainties refer to the quality of complex movements executed in prehistoric times. A modern professional flautist, trained for many years in a music academy, arrives at a very high degree of spatial and temporal precision whilst executing forked movements. When examining woodwind players attempting simultaneously to lift a finger from one hole and touch a second with another finger, they usually complete one movement before starting another; but this overlap amounts to less than 10 ms on average.[24] Flute players are trained to minimise these overlaps in order to avoid slurs, gaps or unpleasant noises degrading the presently dominating aesthetic quality of the resultant performance. In prehistoric times, performances with bone flutes were most probably not bound to these kind of aesthetic judgements, allowing a much more imprecise execution of the complicated finger movements. As an analogy with the term 'anthropomorphism' one could call the problem arising from the approach cited above 'culturomorphism', which transfers implicit present cultural standards to historical or even prehistoric times.

In conclusion, about 35 000 years ago, theoretically highly complex finger movements specific to music-making and similar to those of modern instrumentalists could have been part of the repertoire of prehistoric musicians. Yet, since our knowledge about how music was executed in Palaeolithic hunter-gatherer societies is very rudimentary, considerable uncertainties remain. It is intriguing to speculate that the bone-flutes were the catalysts for evolving 'forks' and similar advanced hand skills during subsequent millennia.

5. MORE CERTAINTIES: SENSORIMOTOR SKILLS OF MUSICIANS IN HISTORIC TIMES

He was an extraordinary virtuoso: he created miraculous effects never heard before on his piano, he even changed the whole character of this instrument profoundly (Camille Saint-Saëns about a performance of Franz Liszt)

It is clear that more certainty about manual skills can be obtained when collecting information from paintings of musicians playing their instruments. There is a large body of literature in the field of archaeology of music concerning this topic which will not be reviewed here.[25] Particularly relevant contributions come from the pictures of playing positions of harpists in ancient Egypt. When looking at the finger positions, different levels of complexity of motor programs can be deduced. Obviously, a rich repertoire of finger movements was used, ranging from playing with predominant use of the thumb and index finger, to playing with both hands and all fingers in a wide range.

Certainly, as is the case nowadays, different techniques may have dominated at different times and places.[26] From the viewpoint of music physiology, some of the paintings exhibit a remarkable knowledge concerning injury-preventing postures of the wrist and fingers. An example of a biomechanically optimal posture of the lower arm, wrist and the fingers is given in Fig. 2.

The female harpist avoids exaggerated flexion and extension of the wrist as well as ulnar or radial deviation. Such a wrist position minimises friction of the finger tendons in their tendon sheaths and allows maximal speed of repetitive movements of single fingers. Furthermore, in this way, pressures in the carpal tunnel and the ulnar wrist tunnel are kept minimal, preventing any traumatising compression of the median or the ulnar nerves in the wrist region.[27] Finally, the fingers are slightly flexed in a very elegant way in all three finger joints, allowing the most effective transmission of forces to the tip of the fingers where the strings have to be plucked.[28] When looking at these postures one is struck by their modernity. The paint-

22 Elliott and Conolly 1984.
23 Kunej and Turk 2000, 265.
24 Altenmüller et al. 2002.
25 See for example the collection of outstanding papers in E. Hickmann, I. Laufs and R. Eichmann, 2000.
26 For reviews on this topic see H. Hickmann 1954 and 1961; Krah 1991.
27 Norris 2000.
28 Kenyon and Thaut 1998.

ings could be integrated in a textbook of modern harp-playing. As with the bone flutes, we do not know their unheard melodies, but there are at least no visible reasons why these musicians would have been less skilled manually than our contemporary harp-players.

Definite conclusions about manual skills of musicians cannot be made until the advent of musical notation and preserved witnesses about the quality of the execution of music supplied by contemporaries. In Baroque times, outstanding musicians and performers like Johann Sebastian Bach or Domenico Scarlatti composed extremely demanding music, which in some aspects reach the limits of technical feasibility even for highly specialised virtuoso performers of our days. When taking the Goldberg Variations of Bach as an example, its execution demands exceptional technical skill in some aspects, for example concerning the rapidity of trills and passages or the precision of bimanual co-ordination. However, later performing composers like Liszt, – who was an excellent interpret of Bach's piano music – used these technical refinements as a basis and added further technical difficulties, for example a novel leap and repetition technique to realise his musical visions. In a very informative article, Lehmann and Ericsson convincingly demonstrate the increasing demands on manual skills in musicians over the past three centuries.[29] According to these authors, the technical challenges are paralleled by the developments of musical instruments, which in turn in many instances were initiated by outstanding performing composers. An example is the extension of range (number of notes) of the piano. In the 18th century alone, the tonal range of the piano grew from four to six octaves. Beethoven requested larger tonal ranges from his piano maker. The same was true for Franz Liszt, who finally arrived at the 'modern' range of eight octaves in the 19th century. A similar extension is documented for other instruments, such as the recorder, the violin and the flute. Additionally, innovations in playing techniques of performing composers added complexity to required manual skills. The 'third hand' technique for example, developed by the pianist Sigismund Thalberg in the 1830's involves distributing the melody notes between the hands in the middle of the keyboard, whilst the accompaniment is played in scales and patterns to the left and right side of the melody. This technique destroys not only the classical mapping of hands onto the keyboard with the right hand playing the melody while the left provides the accompaniment, but additionally requires maintenance of dynamic differences between the melody and the accompaniment within one hand, this way imposing heavy skill requirements on the performer.[30]

The increasing refinement of musicians' manual skills during the last three centuries is well documented. However, the question remains open, whether this improvement is due to early specialisation and longer cumulative practice times or whether other factors such as the instructional strategies may have had a crucial impact on the acquisition of manual dexterity. When analysing the technical skills of child prodigies performing keyboard music in public from the times of Bach until the twentieth century, Lehmann and Ericsson[31] come to the conclusion that during this time span an acceleration in the acquisition of performance skills took place. In other words, there is a significant tendency for prodigies of more recent generations to play technically more difficult pieces after shorter periods of training than did earlier prodigies. Several factors contribute to this effect. Firstly, over the centuries there is a tendency towards earlier commencement of musical training. Not uncommonly, outstanding contemporary performers start their systematic training at ages younger than six years.[32] Secondly, accumulated procedural knowledge of the most effective teaching methods handed down from generation to generation of performer/teachers may have resulted in an optimisation of training methods. Thirdly, due to the specialisation of young performers, who focus on only one instrument, and neglect other activities, there is increased time spent preparing for performances. Anecdotal evidence for the latter notion is abundant from the 19th century on. The pianists Clementi and Czerny are said to have practised eight hours daily already as children in 'solitary confinement' at the piano, Kalkbrenner for 12 hours and Henselt even for 16 hours.[33]

In summary, it is indisputable that the demands on manual skill for the reproduction of composed 'serious' music increased continuously from Baroque times until the middle of the 20th century. It is not only the complexity of movement patterns, but also the elements of tempo, the strength, the stamina and the precision of hand and finger movements which constitute this process of increasing perfection over the centuries.[34] Modern society in turn imposes heightened pressures on performers of composed music by comparing the individual live performance in concert with recordings of outstanding peers, easily available on

29 Lehmann and Ericsson 1998.
30 Lehmann and Ericsson 1998.
31 Lehmann and Ericsson 1998.
32 Ericsson et al. 1993.
33 Gellrich 1992.
34 Wagner 1988.

CDs. Additionally, studio recordings with the possibility of obtaining and splicing multiple takes contribute to an illusionary perfection as standard. All of these changes are reflected in the intensification and prolongation of daily practice. However, one should keep in mind that this development holds only for a relatively small group of musicians, namely the highly specialised classical musicians in the Western cultures of 'serious' classical music. The majority of musicians all over the world are either amateur players, playing their instruments in various social contexts, or professionals relying more on improvisational skills (for example in jazz music) or on the technical developments of instruments and electronic equipment (for example in rock and pop music).

6. NEURAL BASIS OF MODERN EXPERTISE AND THE END OF AN EVOLUTION?

I must practice, practice, practice – the more I advance, the more I must practice
(Svjatoslav Richter, Russian Concert Pianist 1984)
Der dritte Finger scheint wirklich incorrigibile
(Robert Schumann, Diary, 13. 6. 1831)

Intense practice and specialisation of musicians is reflected in structural and functional adaptation of the nervous system. Comparison of the brain anatomy of skilled musicians with that of non-musicians shows that prolonged instrumental practice leads to an enlargement of the hand area in the motor cortex.[35] This enlargement appears to be particularly prominent in all instrumentalists who started to play prior to the age of ten years. Furthermore, in professional musicians, the normal anatomical difference between the larger, dominant (mostly right) hand area and the smaller, non-dominant (left) hand area is less pronounced when compared to non-musicians. These results suggest that the functional adaptation of the gross structure of the brain occurs through training at an early age.

Similar effects of specialisation have been found with respect to the size of the *corpus callosum*, the large inter-connection between the two cerebral hemispheres. Professional pianists and violinists tend to have a larger anterior (front) portion of this structure, especially those who started prior to the age of seven.[36] Since this part of the *corpus callosum* contains fibres related to motor execution, it seems plausible to assume that the high demands on co-ordination between the two hands, and the rapid exchange of information may either stimulate the nerve fibre growth – the myelination of nerve fibres that determines the velocity of nerve conduction – or prevent the physiological loss of nerve tissue during infancy and adolescence.

However, it is not only motor areas that are subject to anatomical adaptation. By means of magnetoencephalography (MEG), the number of nerve cells involved in the processing of sensory stimulation in individual fingers can be monitored. Using this technique, professional violinists have been shown to possess enlarged sensory areas corresponding to the index through to the small fingers of the left hand.[37] There was no difference in thumb representation from that of non-musicians. Again, these effects were most pronounced in violinists who started their instrumental training prior to the age of ten.

In summary, the central nervous system adapts to the challenging demands of modern professional musicianship related to prolonged training. These adaptations are based on **brain plasticity**. If training starts at an early age (before about seven years), this adaptation affects brain anatomy in terms of the enlargement of certain brain structures involved in the respective skill. If training starts later, it modifies brain organization by wiring neural networks and involving adjacent nerve cells to contribute to the required tasks. The neural reshaping of central nervous hand representations begins after such short time intervals as 20 minutes of practice[38] and continues during practice, resulting in enlarged cortical representations of, for example, specific fingers within existing brain structures.

There is a dark side to the increasing specialisation and prolonged training of modern musicians, namely the loss of control and the degradation of skilled hand movements, a disorder referred to as **musicians' cramp** or focal dystonia. The first historical records appear 1830 in the diaries of the ambitious young pianist and composer Robert Schumann. As a private student of Friedrich Wieck, the father of his later wife Clara, he was engaged in a heavy curriculum of daily piano practice of about eight hours. In his diaries, we find initial remarks about a certain loss of regularity in scale playing with the right hand in 1830, later complaints about a lack of control of the middle finger, increasing tension and a tendency of involuntary flexion of the middle finger, which he tried to overcome with a stretching device, the 'tobacco-machine'. Finally, after three years of struggling with the problem he gave up piano playing and concentrated his energies on composing.[39]

35 Amunts et al. 1997.
36 Schlaug et al. 1995.
37 Elbert et al. 1995.
38 Bangert et al. 2001.
39 Schumann 1833.

In present times, approximately one in 200 professional musicians suffer from such a loss of voluntary control of their extensively trained, refined, and complex sensorimotor skills. In most cases, focal dystonia is so disabling that it prematurely ends the artist's professional career.[40] Subtle loss of control in fast passages, finger curling (cf. Fig. 3), lack of precision in forked fingerings in woodwind players, irregularity of trills, sticking fingers on the keys, involuntary flexion of the thumb contacting the bow in strings, are the various symptoms that can mark the beginning of the disorder. At this stage, most musicians believe that the reduced precision of their movements is due to a technical problem. As a consequence, they intensify their efforts, but this often only exacerbates the problem. Males (83%), classical musicians of a younger age (89%), and instrumentalists such as guitarists, pianists and woodwinds (together 70%) are among the most commonly affected by focal dystonia. The majority of patients have solo positions and often have a perfectionist, control-type personality. About 30% of such patients report a history of chronic pain syndromes or overuse injury. The probability of developing focal dystonia increases with the intensity of practice. Therefore, focal dystonia is under certain circumstances acknowledged as an occupational disorder.

Although the neurobiological origins of this disorder are not yet completely clarified, it is probable that musicians' dystonia is in most cases part of a cortical sensorimotor mislearning syndrome, which in turn is due to **dysfunctional brain plasticity**. Support for this theory comes from a functional brain imaging study performed in musicians with focal dystonia (Fig. 4). Compared to healthy musicians, the dystonics showed a fusion of the digital representations in the somatosensory cortex, reflected in the decreased distance between the representation of the index finger and the little finger when compared to healthy control musicians.[41] Such a fusion and blurring of receptive fields of the digits may well result in a loss of control, since skilled motor actions are necessarily bound to intact somatosensory feedback input.

Considering

1) the historical advent of the disorder in the 19th century with rapidly increasing technical demands imposed on musicians,
2) the epidemiological data with cumulative life practice time as a risk factor, and
3) neurobiological findings of the blurring of hand representations, one is tempted to state that focal dystonia finally marks the natural limits of a million years long process of refinement of manual dexterity.

7. CONCLUSIONS: MUSICAL SKILLS OVER THE TIMES IN THE LIGHT OF NEURAL PLASTICITY AND THE EXAPTATION THEORY

With our hands and brains we will achieve what we can achieve – but not more.

In conclusion, we have to answer the questions raised in the first paragraph. The time machine with the expert piano teacher from a renown German music academy arrives with his Steinway D Grand Piano 3500 years ago in the valley of the river Nile in the Temple of Luxor. With his large suitcase full with purposely selected piano music of Hanon, Czerny, Bach, Beethoven, and with Franz Liszt's complete piano works, he waits between the papyrus columns in the dusky Hypostyle Hall of the Court of Amonhotep III. What might happen in this somewhat surrealistic scenario? Whilst intoning one of his favourite piano pieces appropriate to overwhelm the listeners in the grandiose acoustics – Maurice Ravels' Jeux d'Eau –, the priests approaching shyly. The huge black box attracts the interest of the audience and the high priest is making gestures, asking for the opening of the heavy lid of the large black piano. The lid is finally opened by a group of slaves. A murmur raises: "It's just a harp, nothing else than a huge harp, imprisoned in a wooden box, it's a harp making these strange noises!"

Finally, no experimental subject will probably be found to practice on this black box for ten years in order to play the music of the future — and the piano teacher will return with his time machine, his grand piano, his suitcase full of music, and he probably will embark on a second career as an egyptologist. After all, I have no doubt that the young son of King Amonhotep III, if started at age four with our German professor to play on the black box could have learned the Liszt Sonata, given that he was endowed with enough passionate motivation for the approximately 10,000 hours of training required, and given that he had access to a protein rich diet to develop large bones, robust muscles, and hands flexible enough to span the tenths. Similarly, I believe that even much earlier, about 50,000 years ago, a flute player in the Divje Babe I cave could have used his bone flute to interpret the 'Badinerie' of Bach's b-minor Suite after sufficient training with the master flautist J. J. Quantz.

40 Altenmüller 2001, Lim et al. 2001.
41 Elbert et al. 1998.

According to paleo-neurological findings, the brain's macroscopical structure has not changed significantly in the last 100,000 years. The true 'revolution' which enabled *Homo sapiens* to master novel tasks occurred much earlier in human evolution. It was enabled by the development of neural plasticity, the potential to adapt to new environmental stimulation and to new challenges by modification of neural networks – and this potential was most likely present long before the first musical instruments were developed. As has been demonstrated in the preceding paragraph, the musicians' brain is an excellent paradigm to study the short-term and long-term effects of central nervous **neural plasticity** and long term adaptation in sensorimotor systems, even in macroscopical brain structures. Furthermore, in the case of focal dystonia, neuroscientists have become aware of the limits of these adaptations under certain stressful conditions.

Neural plasticity is not only important for brain **adaptation**. It is also an important **'exaptation'**. With the term 'exaptation', Gould and Lewontin[42] denote the emergence of new skills that are developed by exploiting in a totally new way resources that had been selected for other purposes. Deacon showed that the evolutionary expansion of the human brain occurred selectively in the association cortices of the parietal, temporal and prefrontal regions and not in the primary areas, which are mainly involved in the basic processing of incoming stimuli and executive motor functions.[43] As a result, the human brain acquired numerous neural circuits that are not closely tied to specific sensory or motor function. Through the flexibility offered by neural plasticity these circuits were open to acquire non-innate skills linked to tools or musical instruments. In a more general framework, Skoyle argues that the most obvious exaptations are the acquisition of novel skills linked to technology and notational systems such as reading, mathematics and computer programming[44] – and we may add, music-making.

And how will the musicians' manual skill develop in future? Lehmann and Ericsson close their contribution with some noteworthy remarks about the future achievements of musicians: "Given the sophisticated instruments of today, established training methods, early starting ages for practice, and high levels of daily deliberate practice among young musicians, it is tempting to believe that the present generation of élite solo performers may have already reached the ultimate level of mastery of their instruments – a level that cannot be surpassed but only matched by future generations. However, such claims have been made before in the history of music … Considering the unpredictable and creative nature of past achievements in music performance, it is reasonable to assume that as long as society offers appropriate incentives and élite performers keep striving to surpass the achievements of current and past masters, creative innovations will never cease to be made".[45]

It is beyond any doubt that creative innovations will continue on to be made, but as far as manual skill of the independent use of the fingers is concerned, it seems that a final point in a million-year long development was reached somewhere between the beginning and the middle of the 20th century. For the piano, the works of late romantic performing composers such as Rachmaninow, Godowski, Albeniz, and Alcan with their extension of the Lisztean technique mark an end point for the age of virtuosos. When comparing the available recordings, contemporary performers do not seem to be essentially superior to the previous generation.

The new challenge in performing compositions of the 'classical' modern composers, for example of Messiaen, Boulez, Ligeti, which are all extremely difficult to master, is not based in new demands on manual skill, but rather in their complex musical structure and novelty of rhythmic and harmonic patterns. Since these patterns are as yet usually not integrated in the systematic training of music students, they seem extremely demanding, however, they do not present a new qualitative or quantitative challenge in respect to manual dexterity. Many contemporary composers try to overcome the natural limitations of hand skills by exploiting unusual ways of producing sound, such as plucking the strings in the piano or using the open holes for glissandi in the flute. Again, these new techniques can be interpreted as an 'exaptation' of the way of using tools and they may also challenge manual dexterity in a new way, but they do not add new complexity to the independent use of fingers as was for example the case with Thalberg's third hand technique. Another aspect is important concerning future developments: A majority of music enthusiasts feel uncomfortable when exposed to contemporary music and many of them feel unable to judge the quality of the performance. As a consequence they may have difficulties in perceiving outstanding perfection and will not reward extraordinary manual skills as was the case in earlier times. In other words, society will cease to offer appropriate incentives for performers to study these pieces for months or even years.

42 Gould and Lewontin 1979.
43 Deacon 1990.
44 Skoyle 1997.
45 Lehmann and Ericsson 1998, 90.

After all, we suggest that manual dexterity has reached the end of adaptation and exaptation – at least in the conventional style of music making. The advent of disorders such as musicians' cramp may well be a warning sign of biological limitations in individuals, who are especially susceptible to disturbances in neural plasticity. But it is not only pathology or the maximal available accumulative time of optimal training which limits the 'artistic' aspect of musical performance – it is the fact that society wants to feel the need to communicate behind the fingers, the original personal expression of emotional experience. The latter, of course, has to be collected somewhere outside the practising room, limiting the time assigned for manual exercises in a natural way.

In conclusion, with our hands we will achieve what we are able to achieve – but not more. After having reached the summit of manual skills, we will proceed to form and design our instruments according to our abilities including adaptations and exaptations – however, the neuro-biological origin of *Homo sapiens* will remain a part of our existence and thus of our limitations.

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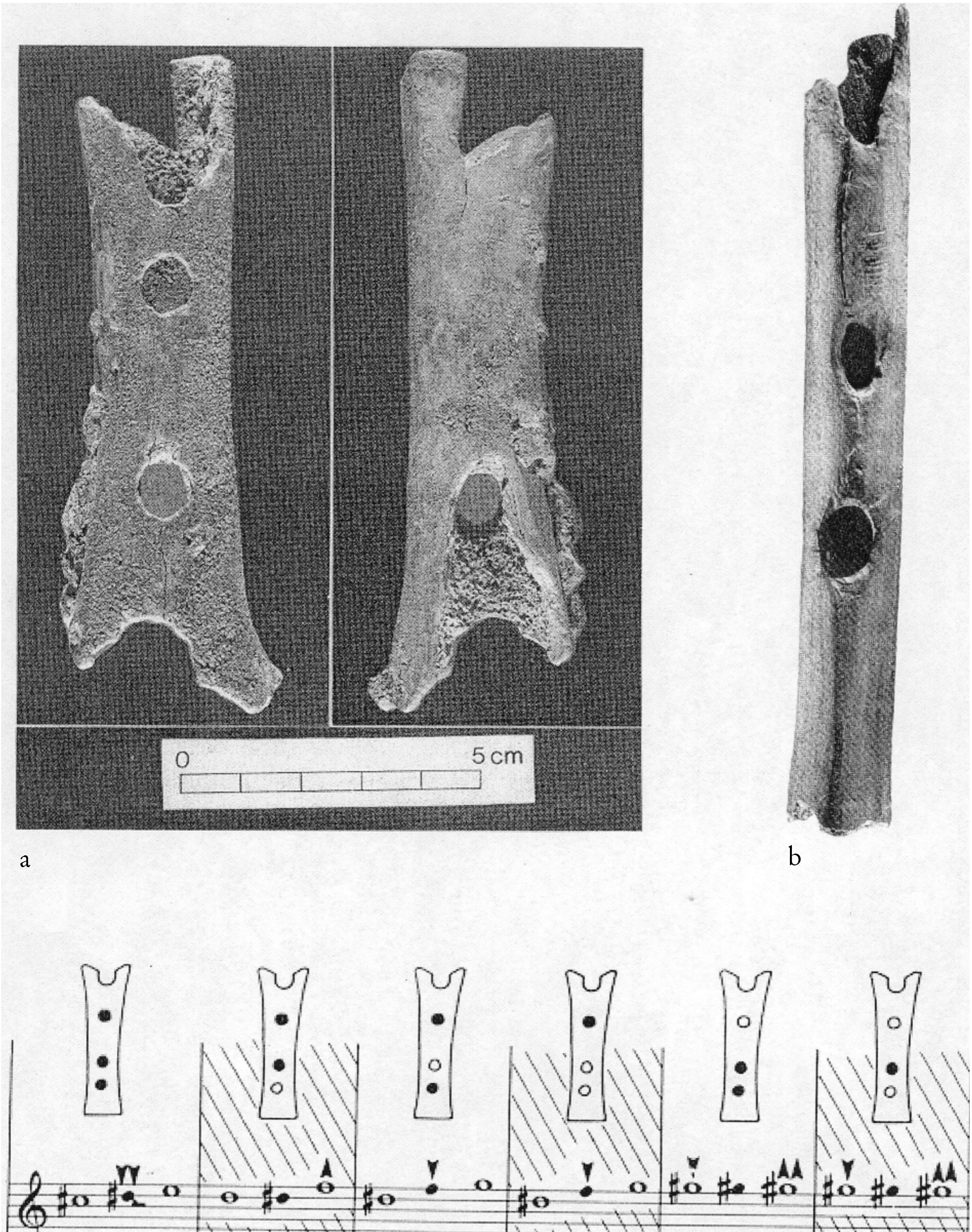

Fig. 1 a. Presumed bone flute from the Divje Babe site in Slovenia dating back to the middle Paleolithic (50,000–35,000 years B.C.). Posterior (left) and anterior (right) views (from Kunej and Turk, 2000 with permission).

b. Bone Flute from the French Cave of Isturitz, dating back to the Aurignacien (35,000–15,000).

c. Fingering table and obtained tones from a reconstruction of the Divje Babe flute. The flute is played with the index, middle, and the fourth finger. A typical forked movement pattern is the combination of the fingerings no. 3 and 6 (from the left), requiring the index and forth finger to be extended, whilst the middle finger is synchronously flexed (modified according to Kunej and Turk, 2000). Similar fingering tables can be designed for the bone flute in Fig. 1 b.

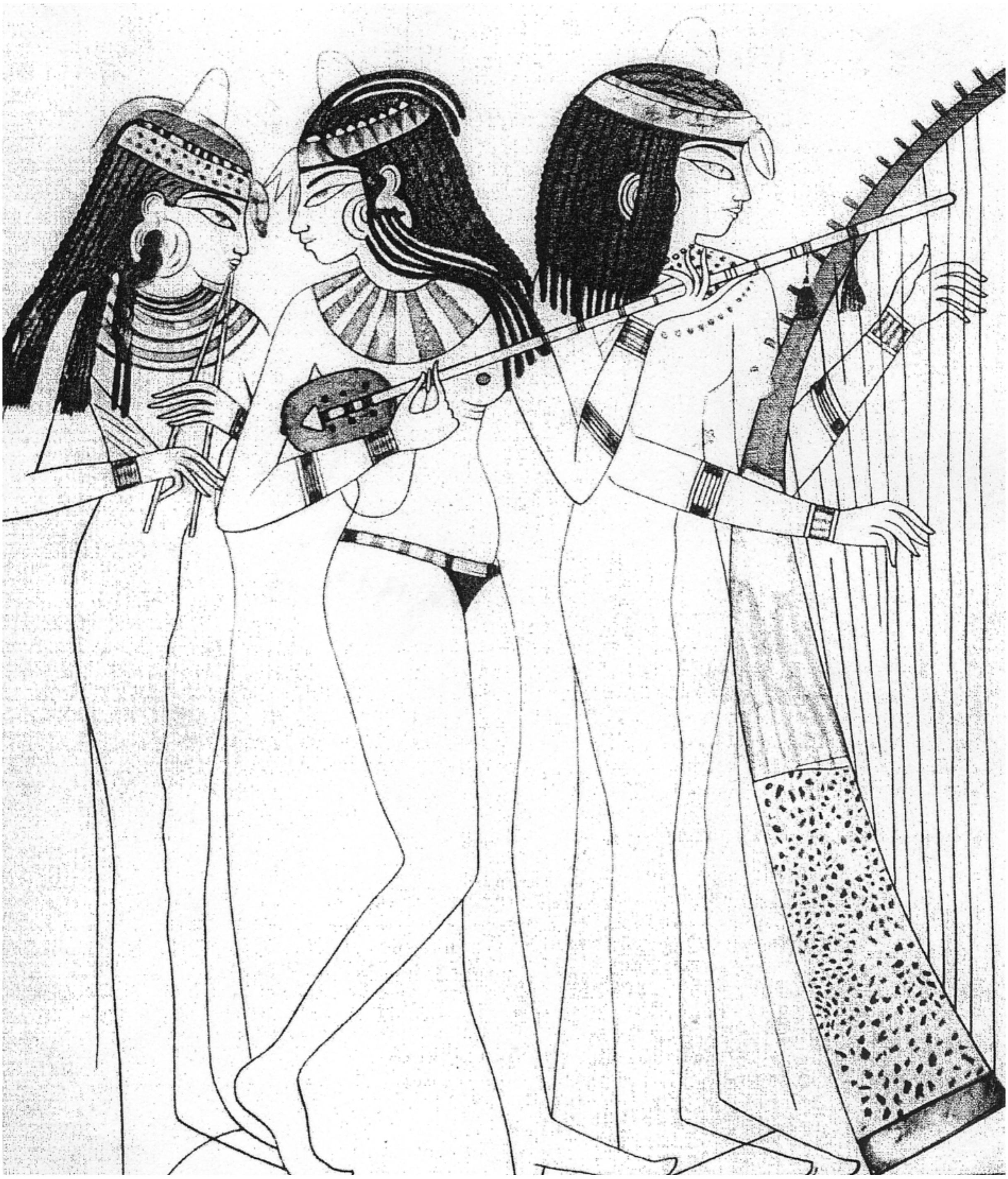

Fig. 2 Redrawing from a wall painting from the 'Tomb of Nacht' in Thebes, Period of Thutmosis IV, 1425–1405 B.C., showing a group of musicians with double oboe, lute, and harp. The wrist postures of the harpist are ergonomically optimized. She is picking the strings with the right index or middle finger, whilst the left hand presses the string down, in this way shortening the string (from H. Hickmann, 1961, 99).

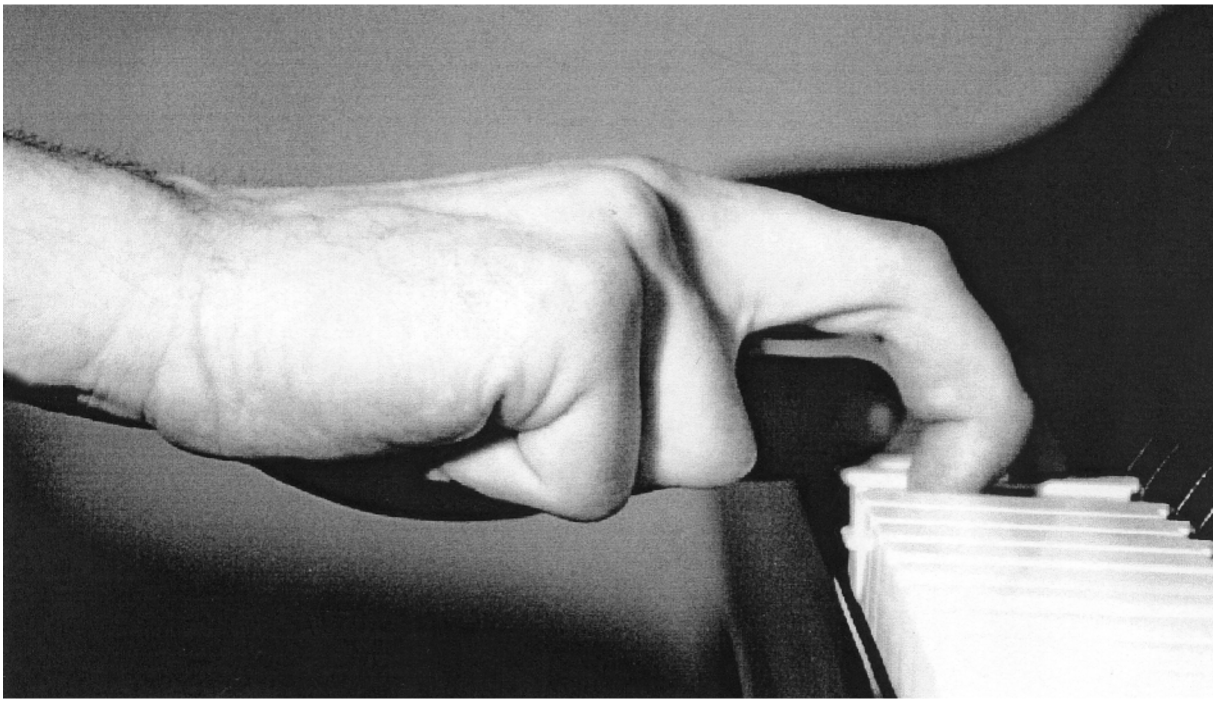

Fig. 3 Typical example of a dystonic movement patterns in a pianist. When playing a c-major scale upwards and touching the key with the third finger, the fourth and fifth fingers are cramped involuntarily, resulting in a 'curling in' movement.

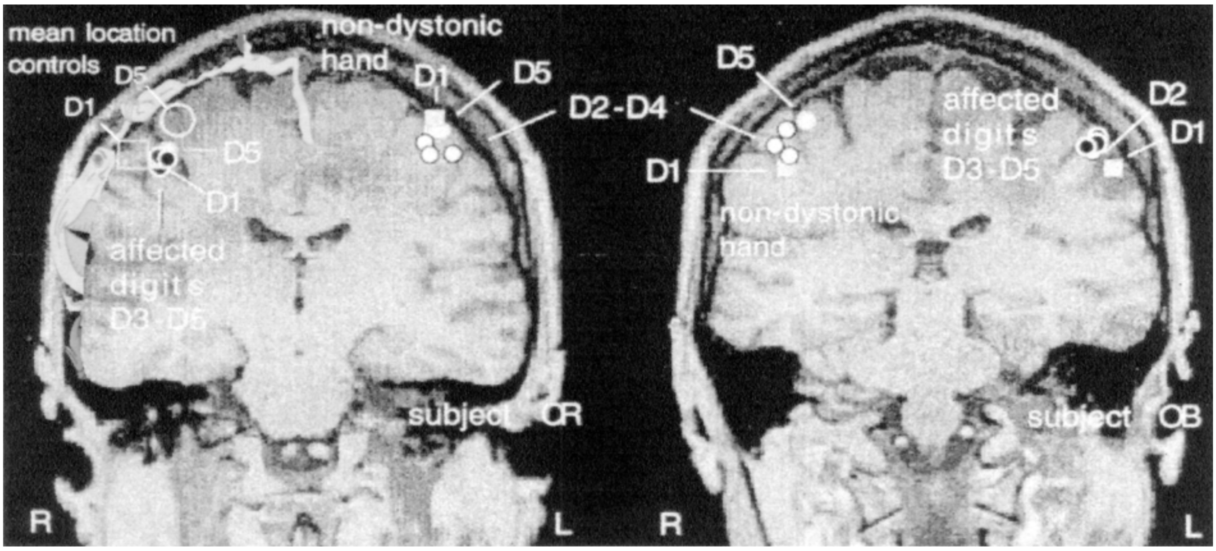

Fig. 4 Fusion of the somatosensory representation of single digits of the hand in musicians suffering from focal dystonia as revealed by Magneto-encephalography (MEG) and Magnetic Resonance Imaging (MRI). MRI sections through the somatosensory cortices of 2 musicians suffering from hand dystonia are shown. The responses of evoked magnetic neural reaction potentials following sensory stimulation of single fingers are displayed. The responses of the digits 1–5 (D1–D5) code for the neural networks involved in somatosensory processing of individual fingers. Whilst in healthy musicians the typical homuncular organization (see inset on the left MRI) reveals a distance of about 2,5 cm between the networks processing stimuli from the thumb and the little finger (open circle and square on the left), the somatosensory representations of the fingers in dystonic musicians are blurred, resulting from a fusion of the neural networks which process incoming sensory stimuli from different fingers (black circles). (Modified from Elbert et al. 1998).