REMARKS ON NEUROCONTROL OF THE HAND AND SIGNIFICANCE OF AFFERENT INPUT

KOMENTARJI O ŽIVČNI KONTROLI ROKE TER O VLOGI AFERENTNEGA DOTOKA

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Abstract – *This paper outlines some remarks on our understanding of motor control of the hand. It begins with current knowledge about motor behavior of prehension movements. It further highlights the distributed nature of the control system that integrates sensory information from the periphery, existing motor memory from subcortical centers, and information from diverse primary and secondary motor as well as sensory areas. It further explains the sequential nature of the processes like decision, planning, computing, and execution involved in neurocontrol of a purposeful hand motor task. In the successive part it stresses the importance of sensory input, in particular proprioceptive, for movement setting and guidance. It concludes by pointing out research concepts used to study roles of sensory information for modulating states of neurobiological systems. Finally, a novel method of whole hand electrical stimulation, which seems promising as a tool for studying sensory-motor integration mechanisms in human's hand, is explained and recent experimental data are provided.*

Izvleček – *Članek podaja nekatere komentarje našega razumevanja o kontroli gibanja roke. Začenjamo s podajanjem trenutnega znanja o motoričnem obnašanju in izvajanju gibanja. Sledi razlaga kompleksne narave kontrolnega sistema za gibanje, ki združuje periferne senzorične informacije, obstoječe gibalne programe motoričnega spomina subkortikalnih centrov ter informacije različnih primarnih in sekundarnih kortikalnih področij, tako motoričnih kot senzoričnih. Nadalje opisujemo sekvenčno naravo procesov, kot so odločanje, načrtovanje, oblikovanje odgovora in izvedba, ki se združujejo v procesu kontrole izvedbe smiselne motorične naloge. V poglavju, ki sledi, je poudarjen pomen senzoričnega dotoka, s poudarkom na proprioceptivnem, pri oblikovanju in vodenju giba. Prispevek je sklenjen z opisom raziskovalnih pristopov za proučevanje vloge, ki jo imajo senzorične informacije pri spreminjanju živčnih sistemov. Končno je predstavljena metoda električne stimulacije cele roke, ki se zdi obetavajoča metoda za raziskovanje senzorično-motoričnih integracijskih mehanizmov roke.*

Introduction

Aristotle described the human hand as 'an instrument that represents many instruments'. Whereas other animals have limbs specifically shaped for climbing, running, flying, swimming or hanging, humans have different specialization and particularly this is the case in the human hand. Diversely, the human hand has developed for a range of activities. It is the perfect all-purpose tool, the Swiss Army knife of limbs, so adaptable that it solves problems such as hunting, running, flying, swimming, and so on, by making machines that do all those things. It needs of course, to be connected to a brain that can control such a tool, but the brain would also be far less useful without such a hand connected to it. Brains and hands co-evolved (1).

On the other hand it is remarkable what a role sitting plays in manual skill. This relation has been illuminated by Phillp V. Tobias in his essay titled »Man, The Totteting Biped: the evolution of his posture, poise and skill« (2). In his opinion, bipedalism was not a prerequisite either to effective tool using or to rudimentary tool making, while there are also other circumstances under which a creature's hands are freed. In fact, most implemental activities of man and of great apes are carried out in sitting position in which our bodies find high level of stability. The later is of basic importance in the development of manual skill.

However, a picturesque example of human deprived of locomotion but able to sit reveals how hand skill potentials can be expressed. This is the case in paralyzed people due to neuromuscular disorders. Namely, manual skills for controlling computers and variety of devices, not to mention skills of art, continue to be present for reproduction of brain capabilities. If we provide support for taking advantages of brain-hand expression in people with paralyses they become independent. In short, previously disable can through brain-hand capacity demonstrate new abilities.

Anyhow, the function of the upper extremity in humans is unique when compared to the function of the forelimb of other mammals and even to that of primates. The human upper extremity is fully independent from locomotion in a body that's skeletal, muscular, and nervous system control is able to generate long standing and bipedal locomotion. The arm and hand are thus devoted to the exploration of extra- and intrapersonal worlds. Life is full of well defined hand movements which can be divided into topokinetic movements (shaking hands, reaching a latch or a glass of water) and morphokinetic movements (writing or drawing). Control of the arm, hand, and fingers is part of expressive communication behavior and is requirement of acceptance into human society. The hand is also important in expressing emotions through painting, music, and drama (3).

Besides having different musculoskeletal design than the lower extremity, the arm and hand are subject to more complex neural control. Before initiating a purposeful motor act such as grasping an object, the nervous system needs information. Vision describes the shape of the object, its location, and its distance from the body. Proprioceptive input defines the condition of the inner world and the position of the limbs and trunk. The brain searches for stored memories of similar situations. Once the object is touched, cutaneous proprioceptive sensation updates the recorded memories of weight, surface, and shape.

The purpose of this paper is to give an overview about neural control of the hand and significance of the afferent input. We will review hand motor control related issues like peripheral receptors as a base for kinesthesia, role of sensory feed back for on-line movement control, planning and execution of a hand motor act potentials to use afferent manipulations to improve motor control.

So we move our hand

However, through daily activities we are not aware that this implementation of our upper extremity is a part of complex underlying neurobiological mechanisms of neurocontrol. The research of motor control has been developed and today this field covers a wide variety of approaches used to study human movements, such as hand motor tasks. It all began with observations of behavior using static techniques such as photographs (4), over introduction of high-speed cinematography (5) to neurophysiological measurements. In Lemon's opinion the biggest advance in studying motor control of the hand has come from realization of the fundamental need for start observing natural movements. Pioneering work (6) based on complex motor tasks was amenable to in-depth quantitative study. In spite of this fact motor system physiologists believed for many years that only simple fractures of a movement could be analyzed and understood. Almost all the work carried out was considering single joint system and how it operates. Nevertheless, this is very abstracted model to observe and is far away from the real situations of everyday life. From the early seventies on, introductory physiological studies presenting natural movements emerged. Thus, we were introduced the precision grip (7), pointing tasks (8), precision lift (9), reach and grip task (10, 11). Since than, all these have been serving as tools to study normal as well as changed physiology (12–15). During the recent years, the repertoire of the listed movements with which a human or an animal explores external and internal environment was enriched by some additives. Wing and Flanagan (16–19) have been exploring brisk alternative arm movements during grasping an object while bimanual 'draw task' was observed by Wisendanger (20).

Probably the most fundamental hypothesis was proposed by Jeanerod, speculating about the existence of two major components responsible for the guidance in grasping movements: (i) the transportation of the hand to the vicinity of the object to be grasped and (ii) the formation of the particular posture of the fingers (Figure 1). Testing the degree of independence of each component of motor control is critical for evaluating the existence of transport and hand-shaping subunits. Based on studies that were systematically changing entities of an object a subject was reaching (21, 22) or position of it in space (21, 23, 24), re-examination of the proposed existence of the two movement components, transport and grasping, was confirmed. To sum up, the argumentations above suggest that the two components of prehension are controlled by diverse pathways. Although the two mechanisms for preshaping and transporting the hand, respectively, lie close to each other in the posterior parietal cortex, they can be dissociated by lesions (25).

Figure 1. *Reaching to grasp representing how transport and manipulation components are affected. Note the anticipatory opening of the hand that is appropriate for an object to be grasped. At the same time transport subcomponent remains unchanged.*

Where the movement came from?

Thus, when a voluntary movement of the hand is to be brought forth, numerous parallel as well as sequential integrative sensory-motor processes are taking part. Like our perceptual skills reflect the ability of sensory systems to detect, analyze, and differentiate certain physical stimuli, our dexterity indicates the capabilities of the motor systems to plan, coordinate, and execute movements. In fact, these two systems are inseparable. They rather operate in a complementary manner, though both organized within brain and spinal cord. Just as there are different modalities of sensation, there are three diverse categories of movement – reflexive, rhythmic, and voluntary. While human hand's primary role is to make explorative and manipulative motor acts, we will explain its motor control using an example of a voluntary movement.

So, motor systems operate inversely to sensory ones. Motor processing namely, begins with an internal representation and cognition of the movement, within brain mechanisms. Instead of thoroughly reviewing anatomical and morphological features of diverse parts of components of central nervous system involved in setting and execution of a purposeful voluntary hand movement, we will rather consider their functional roles. Voluntary movement is organized in the cerebral cortex, although different parts of it communicate to other cortical areas as well as to subcortical areas, cerebellum, and spinal cord (Figure 2).

The primary motor cortex controls simple features of hand movements and can be selectively activated by repetitive isolated finger tapping (26). Accordingly, primary motor cortex plays a major role as an executioner of goal directed movements. More complex motor activity is interactively planned involving other parts of central nervous system. Major projections to primary cortex come from premotor cortical areas that communicate directly to the spinal cord as well. According to their pathways this part of cerebral cortex is divided into lateral ventral and dorsal premotor areas, supplementary motor area, and cingulated motor areas. Each of them contributes to different aspects of motor planning. The supplementary and pre-supplementary motor areas play an important role in learning sequences of discrete movements. Evidences for this come from EEG studies (27–29) as well as functional imaging (26). In the latter study it has been shown that it is possible to selectively activate medial premotor area when only mental rehearsing of movements in absence of their execution. Additionally, researchers demonstrated increased corticospinal excitability while mental imaging of motor activity without its execution (30, 31). The lateral premotor areas contribute to the selection of action and to sensory-
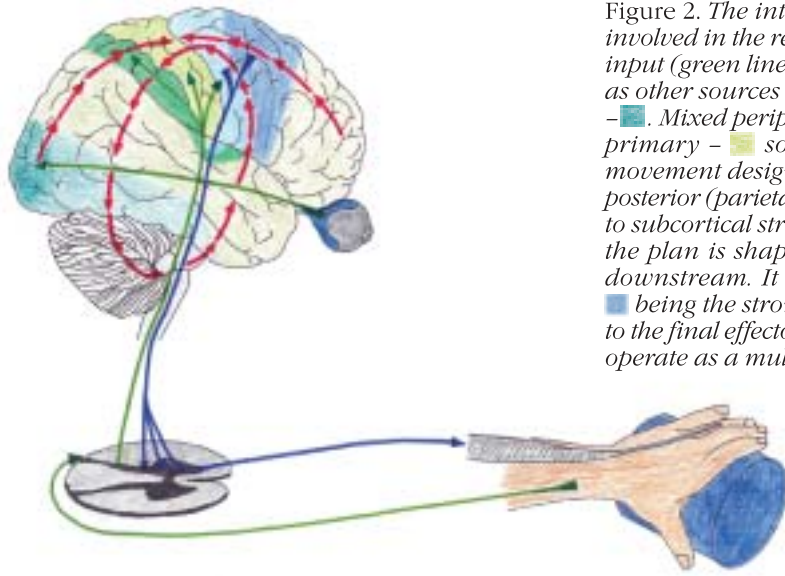
Figure 2. *The interplay between subcomponents of the neural system involved in the regulation of voluntary hand movements. Rich sensory input (green lines) comes from receptors of the upper extremity as well as other sources such as vision. The latter projects to the visual cortex – ▨. Mixed peripheral input projects mainly to the secondary – ▧ and primary – ▨ somatosensory cortex. Planning and shaping of the movement design takes place in areas such as anterior (frontal) and posterior (parietal) association areas – ▨ , that complexly communicate to subcortical structures, cerebellum and spinal cord (red lines). Once the plan is shaped, primary motor cortex – ▨ begins discharging downstream. It again receives various that from premotor area – ▨ being the strongest. Blue lines indicate efferent pathways that lead to the final effector – muscle. As we can see, this regulatory mechanisms operate as a multiparallel system.*

motor transformations. These transformations required for reaching and grasping involve two different pathways from the primary visual cortex to the premotor areas. Interestingly, all of the mentioned cortical areas receive unique and common subcortical inputs. For instance, motor cortex receives inputs from the cerebellum via the thalamus, as well as direct ascendant sensory inputs from periphery (32, 33). Similarly, there are not only direct projections to motoneuron pools which derive from primary motor cortex, just the opposite; there is evidence for such projections from premotor areas. When we reach out to grasp a small object, the first goal is to adequately position the fingertips onto its surfaces in order stable grasp is established. The transport and shaping of the hand reflect a precise coordination through which spatio-temporal parameters for reach and grasp are defined (34). The demand for precise control gradually increases while approaching contact (35) thus the intertrial variability of fingertip position is attenuated.

After the first contact with an object, necessary finger tip force should be produced. This action evolves in a series of phases associated with responses in tactile afferents from the digits (36, 37). The initial contact marks the beginning of the pre-load phase. Load phase, transitional phase, and static phase are afterwards carried out in succession. A specific role of hand sensory organs is to link the various phases of the lifting task by informing the central nervous system about the action flow at the periphery. Finger tip forces are parameterized by implicit memory information of the friction and weight, acquired during previous manipulations of an object (38). Thus tactile input provides information about those two parameters of friction and weight.

The control of grasping and manipulation relies on distributed processes in the central nervous system, engaging most areas to be involved in sensory-motor control (39). During the execution of the task, primary motor cortex is likely the main actor, which is probably most obvious when concerning skilled hand tasks (40). Different subcomponents of the supraspinal neural control of the hand movement can be studied by comparing neural states reached by motor areas. Non-invasive transcranial magnetic stimulation (TMS) enabled researchers to probe cortico-motoneuronal excitability. Additionally, it has been reported that the amplitude of motor evoked potentials evoked by TMS may to some extent be dependent on the level of cortical activity (41–44).

In their communication Lemon, Johansson and Westling (45) report about striking changes in the amplitude of EMG re-

sponses to TMS delivered to the hand area of the motor cortex during different phases of a natural task of reaching, grasping and lifting. This modulation may well reflect brisk changes in corticospinal excitability.

Lemon et als' (45) results suggest that the cortical representations of extrinsic hand muscles, which act to orientate the hand and fingertips, were subjected to a strong supraspinal excitatory drive throughout the reach. This drive was also observed for brachioradialis and anterior deltoid which contribute to transport of the hand. In contrast, the intrinsic hand muscles appear to receive their strongest cortical drive at the digits closed around the object and just after the subject first touched the object at the onset of manipulation.

To infer, tactile inputs are known to be essential for appropriate coordination of this task (9, 36, 46) and therefore possible that this strong effect partly results from a central interaction between these inputs and TMS. Indeed, Johansson et al. (12) have provided evidence that such interactions may occur while subjects respond to small, unpredictably occurring step load increases imposed to an object restrained between thumb and index finger. Accordingly, tactile inputs are known to exert excitatory effects on a large proportion (around 58 percent) of monkey motor cortex neurons related to hand movement (33). To sum up, using natural movements it is possible to demonstrate changes in corticospinal excitability, while the task has been carried out. These changes are likely, at least in part, to be modulated by ascending afferent flow while cutaneous inputs are shown to be strongly implicated in the initiation and scaling of the grip force. For example, in early catch-up grip response (47) cutaneous information was those to initiate the long-latency 'catch-up' grip response (48).

If we conclude, there are sequences of neural processing carried out that finally generate motor information necessary for the execution of a purposeful volitional movement of the hand (Figure 2). Each cortical area receives unique inputs. Visual information from the environment is specifically detected and conveyed to the primary visual cortex. In order this incoming information to be interpreted; it goes further to the frontal cortex. It is a site where planning of the movement takes place and therefore it is an integrative area that receives wide range of inputs. From basal ganglia come 'history information' on what the brain already know about movements like the one to be planned. On the other hand, somatosensory area passes information on proprioception and body scheme. Using all these data a plan for intended movement is shaped and conveyed through premotor areas to the primary motor cortex.

These project downstream to the proper segmental interneurons and motoneurons of the spinal neuron pool. As a result of spatially and temporally coordinated activation of these final neuronal stations coordinated hand movement is born. However, reafference copy of motor cortical output back to parietal cortex and constant afferent refreshment from periphery is crucial for on-line governing of such skilful movement.

Nothing happens without knowing about peripheral state

During the early nineteenth century, philosophical approach named positivism was proposed by Comte who was influenced by British empiricists. They suggested all knowledge be obtained through sensory experience. That is when psychology was seceded from philosophy, the first being concerned with studies of sensory signal and perception. Although objects we reach and grasp are perceived as phenomenal entities, sensory systems are known to detect features not objects (49). The sensory systems of the hand encode four elementary attributes of stimuli – modality, location, intensity and timing. They are all manifested in an integrated sensation. Sensory modality is determined by the form of stimulus energy, so that specific hand receptors transduce specific types of energy into electrical signals. The last are conveyed along spinocerebral pathways crossing different relay nuclei. In 1931 Edgar Adrian and Keith Lucas demonstrated how a sensory nerve, even though it transmits nerve impulses of fixed strength, can still convey a complex message (50). Today we know that complementary sensory systems have a common plan they follow in order to make it brain understand and respond what periphery sees.

Information transmitted to the brain from mechanoreceptors of the hand enables us to feel the shape and texture of objects as well as permits us to execute finely coordinated motor tasks such as threading the sewing needle. According to their location mechanoreceptors can be divided into cutaneous and musculotendinous. The later involves muscle spindle and Golgi tendon organ. Physiologically, muscle spindle is a receptor for muscle length and is unique among sensory organs with its sensitivity being descendently controlled from supraspinal centers. When its function was studied using different methodological approaches, it was recognized that muscle spindle with associated neural connections respond both, to phasic changes in muscle length (tendon-tap reflex) as to tonic input of vibrations (tonic vibration reflex). Anyhow, in both cases afferent input influences agonistic motoneuron pool by means of facilitation. Zoological studies however emphasize

muscle spindle to be paramount designed for detecting vibrations. On the other hand, Golgi tendon organ is a receptor for muscle tension. While it responds to active production of muscle force (voluntary contraction) much more than to passive stretch it is sometimes also considered as a sensor for level of muscle contraction. Under relaxed resting conditions, Golgi tendon organ activation inhibits agonistic motoneuron pool. Touch is mediated by mechanoreceptors in the skin, whereby these differ in morphology and skin location (Figure 3). These receptors are purposefully distributed over the area of a 'skin glove' and hence different sensitivity for different stimulus modalities at various sites of the hand surface (51). Experiments using anaesthesia (52) documented crucial role of cutaneous sensory input for perception of hand body schema and neurocontrol of the hand movements, oppositely such sensory restriction at knee joint caused actually no deficit. On the contrary, joint and muscle mechanoreceptors of the hand seem to play a secondary role.

To reconsider, peripheral sensors are designed to transducer physical energy to nerve impulses, spikes. According to the all-or-none rule, amplitude of an action potential in a single afferent fibre is constant as it once depolarizes. Thus, 'information code' is defined by population of sensory fibres activated and frequency of nerve impulses on one hand (stimulus strength encoded), and by the duration of the input (tonic vs. phasic events). Once generated, this afferent code is conveyed centrally to spinal cord and upstream to supraspinal centers, crossing relay nuclei. Anyhow, interpretation and utilization of this incoming information is dependent on central states at different levels.

The control of upper extremity movement and posture is believed to involve particular neural signals, some of which have access to consciousness. Such signals, encompassed within the terms kinaesthesia and proprioception were originally proposed by Bastian and Sherington and have become virtually synonymous that covered a loose meaning of almost anything concerned with the control of movement. These signals arise from activity in mechanoreceptors, from centrally generated motor commands, and from interactions between these afferent and efferent signals (53). Kinesthesia and proprioception today denote a group of sensations. First is the traditional sensation of position and movement of the limbs and trunk. Second, there are sensations related to muscle force, including effort, tension, heaviness, and stiffness. Third, sensations exist for timing of muscle contractions. Fourth, there is a sensation of body posture and size as a part of a 'schema' enclosing more than one joint. The term 'input' refers to the discharge of afferents from muscle, joint, and cutaneous recep-

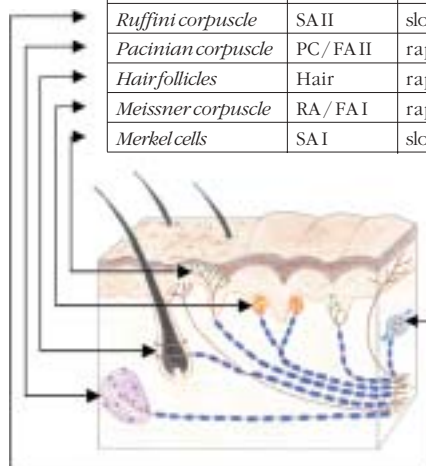| Receptor	Innervation	Adaptation	Modality
Ruffini corpuscle	SA II	slow	moderate, static touch
Pacinian corpuscle	PC / FA II	rapid	light, dynamic touch (vibration)
Hair follicles	Hair	rapid	light, dynamic touch
Meissner corpuscle	RA / FA I	rapid	light, dynamic touch (flutter)
Merkel cells	SA I	slow	light, static touch

Figure 3. *The location and morphology of receptors in hairy and glabrous skin. Note the exact location of different receptors and free endings relative to the distance from the skin surface. Deep receptors have bigger receptive fields as compared to the superficials. Only skin receptors that are most important for the control of hand movements are provided. For more detailed data on the above classification see (54, 55).*

Figure 4. *120-minute subthreshold mesh glove stimulation was evaluated by pre-post measurements using TMS as a diagnostic tool. Standard whole hand mesh glove stimulation was employed by means of common distal anode and cathodes placed on the palmar and dorsal area of the forearm. Botzmann equation was employed to observe changes in corticospinal excitability. Before and after the whole hand conditioning, muscle responses (first dorsal interosseus) to TMS of different intensities were recorded. On the graph above we can see average data for 10 healthy subjects before (solid line for the calculated function and red circles for data at single relative intensity) and after (dashed line and blue triangles). All the key parameters of the mathematical method showed statistically significant modulations of corticospinal excitability after 2-hour whole hand subsensory stimulation; thus left-up shift of the curve (68, 69).*
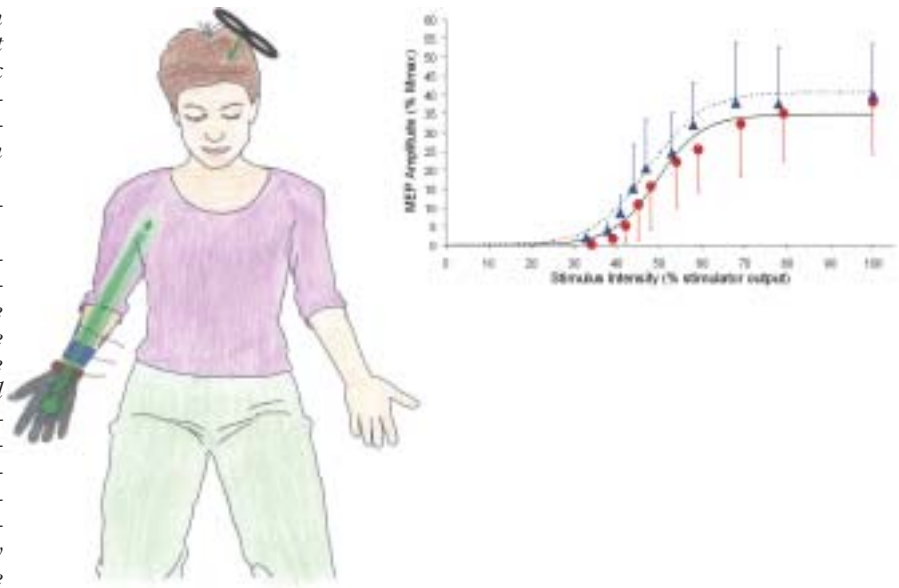
tors. 'Kinaesthetic signals' include the contribution from motor command signals as well as the mentioned inputs. Motor commands encompass the general term corollary discharge as well as the specific form called an efference copy.

There has long been controversy about how to reference kinesthetic signals. It is now clear that limb muscle receptors influence sensations of limb movement just as cutaneous inputs influence sensations of objects on the skin. Appropriate referencing of motor command signals must also occur. As we can see, the full array of specialized muscle, joint, and cutaneous afferents are potential kinesthetic inputs. On the other hand, an afferent class may have more than one kinesthetic role. It is not purposeful to extensively review types of receptors and modalities of information they transfer, while there are clusters of such literature available elsewhere (54, 55).

If we depict a simple scheme for kinesthetic signals, we can say that afferent and efferent kinesthetic signals have no single role, they contribute to kinesthesia and motor learning and they also reflexly change movements. Their contribution to motor control proceeds with or without conscious awareness. In the short and long term, kinesthetic signals mould an adaptive model of the musculoskeletal system (53). Inclusion of sensations of muscle timing and the body schema in the definition of kinesthesia recognizes their essential role in the control of movement.

Hand motor control can be affected using afferent manipulations

As we could see sensory mechanisms through which central system is informed about relative positions of body's parts, the rates of their movements, the forces they exert, and the relative timings of their various contractions, are essential for organization of neurocontrol. Therefore, having controlled artificial access to this input could enable us to control setting mechanisms of the control. Projections of individual types of proprioceptors to central nervous system are inseparable when natural movement is carried out. In order to establish these projections one must be able to excite receptor belonging to that type selectively. This can be done using appropriate mechanical stimulation (56) of the muscle or joint or by graded electrical stimulation of their sensory nerves (57, 58). However, with either technique it is difficult to excite receptors of one type and not other.

To date, different neurophysiological and neuroimaging techniques were used to test effects of electrically evoked by afferent input on activity of various neural structures and their excitability. Excitability of the corticomotoneuronal system is modulated by peripheral afferent stimulation tested by TMS and measured by elicited motor evoked potentials (MEPs). In healthy and adult subjects, both facilitation (59, 60) and inhibition (61, 62) of MEPs have been shown to take place 100 ms following a single electrical stimulus above the threshold for sensory perception given at periphery. On the other hand, decreased motor cortex excitability has been observed at intervals longer than 200 ms (63, 64). Reports are in agreement that in the single conditioning ES paradigm, applied below threshold for perception, there is no modification of corticospinal excitability tested by TMS. There is actually no report on the effect of prolonged electrical stimulation with a train of ES above or below sensory perception on the corticospinal excitability.

Our previous studies (65–67) showed that increased muscle tone and impaired volitional movements of the spastic hand in the spinal cord, head injury and stroke subjects can be ameliorated if the whole hand is stimulated by sustained electrical stimulation (train of 50 Hz, for 30 minutes) below the level for sensory perception. The hand is stimulated by a glove made of conductive wires that act as a common anode to a pair of carbon rubber cathodes placed over the dorsal and palmar surfaces of the forearm (Figure 4). This finding that sustained stimulation of the spastic and paretic hand below perception of tingling sensation within whole hand can induce functional modifications, rise two questions: (i) which structures of the hand are stimulated? Do these externally induced volleys, when the whole hand is target of stimulation, modify motor cortex excitability?

In our recent studies (68, 69) we demonstrated how temporal summation, 50 Hz train for 30 and 120 minutes respectively, of afferent input by stimulus below the level of sensory perception can induce modification of motor cortex excitability (Figure 4). Furthermore, pure spatial summation, whole hand instead of nerve trunk stimulation, of a single conditioning peripheral electrical stimulus however did not affect state of corticospinal tract. It seems so far most possible slowly adapting Ruffini endings are activated by the low intensity mesh glove stimulation, though to induce an effect they recruit need to be fed as a train. Anyhow, until now we can not explain unambiguously what population of peripheral sensory system is recruited by subsensory whole hand stimulation. Namely,

two crucial physiological characteristics are interdependently responsible for what is going to be depolarized first. On one hand, diameter of an afferent fiber that innervates certain sensor – large fibers are depolarized at lower current intensity. On the other hand, spatial relation between stimulation site and underlying neural structure is important. Given electrical current being reduced by square of distance, deep neural structures are going to be much less prone to respond to electrical stimulation applied over skin than those more superficially. Studies in progress will probably clarify, using methods of mathematical modeling, what the precise physical stimulation characteristics of the mesh glove stimulation are and which sites of stimulation are the most likely to be activated. It seems promising for our future research to use the mesh glove as a unique tool to study sensory-motor integration mechanisms of the hand. We namely believe that more functional controlled whole hand afferent input is diversely 'understood' by the brain from that of the stimulation of the nerve trunk.

Moreover, this demonstration how hand receptors' afferents can be stimulated using electrical current of the intensity below the level for sensation, opens a new avenue in the research of motor control. Possibility to modify corticomotoneuronal excitability in such a way seems promising also for other research work such as learning. We are up to ask ourselves some new questions. Can we optimize the execution of a certain motor skill? Can we contribute to faster and more efficient acquiring of new motor skills? At present this is an alternative research direction in motor control which might be leading us to new training procedures useful also for people practicing sports.

Moreover, demonstration of selective external control of proprioceptive and exteroceptive afferent input by the whole hand mesh-glove electrical stimulation provide experimental background for neurophysiological studies of preparatory brain motor control functions. Activation of different regions of the brain activity, after movement was planned by frontal lobe, there is setting phase of brain motor control, consist of distribution of activity within different parts of the brain in order to set components of complex 'code' for execution of the movement. Descending volleys via multi-parallel direct and indirect long brain-spinal cord descending pathways will reach premotor spinal cord network and common final pathway and generate desired skillful or automatic movement. This new possibility to modify proprioceptive skin input at the level below sensory perception by stimulation of the part of the body instead of the nerve trunk it opened new avenue in external modification of the preparatory brain motor functions. Therefore, above described mesh-glove studies in addition to beneficial application to the people with impaired movements due to neurological conditions can become a method for modification of preparatory brain motor control functions in people working toward or practicing improvements of motor performances in the variety of sports.

A poet Sir Philip Sidney once wrote a poem about a group of pre-lapsarian animals who, despite living in a perfect harmony, nevertheless bagged Jove for a king to rule over them (70). Each animal contributed its best part to the new ruler, and so the lion gave its heart, the elephant its memory, the parrot its tongue, the cow her eyes, the fox its craftiness, the eagle its vision, and finally, the ape gave the 'instrument of instruments, the hand'. Since than human's hand driven by the brain enables us to develop ourselves by means of exploration of existing environment as well as creating a new one.

References

1. Peck AL. Aristotle: Parts of animals. London: Heinemann, 1937: 687.
2. Tobias PV. Man the totterig biped: The evolution of his erect posture. In: Garlick DD ed. Proprioception, posture and emotion. The University of the Sauth Wales, 1981: 1–13.
3. Dimitrijevic MM, Soroker N, Pollo FE. Mesh glove electrical stimulation. Science & Medicine 1996; 5: 54–63.
4. Napier JR. The prehensile movements of the human Hand. Bone Joint Surg 1956; 38B: 902–13.
5. Jeannerod M. Intersegmental coordination during reaching at natural visual objects. In: Long J, Baddeley A eds. Attention and performance IX. New York: Hillsdale, 1981: 153–68.
6. Bernstein N. The co-ordination and regulation of movements. Oxford: Pergamon, 1967.
7. Hepp-Reymond MC, Wiesendanger M. Unilateral pyramidotomy in monkeys: Effects of force and speed of a conditioned precision grip. Brain 1972; 36: 117–31.
8. Georgopoulus AP, Kalaska JF, Massey JT. Spatial trajectories and reaction times of aimed movements: Effects of practice, uncertainty, and change in target location. J Neurophysiol 1981; 46: 725–43.
9. Westling G, Johansson RS. Factors influencing the force control during precision grip. Experimental Brain Research 1984; 53: 277–84.
10. Jeannerod M. The timing of natural prehension movements. Journal of Motor Behavior 1984; 16: 235–54.
11. Wing A, Fraser C. The contribution of the thumb to reaching movements. Q J Exp Psychol 1983; 35A: 297–309.
12. Johansson RS, Lemon RN, Westling G. Time-varying enhancement of human cortical excitability mediated by cutaneous inputs during precision grip. J Physiol 1994; 481: 761–75.
13. Sheth BR, Shimojo S. How the lack of visuomotor feedback affects even the early stages of goal-directed pointing movements. Exp Brain Res 2002; 143: 181–90.
14. Favilla M. Reaching movements: mode of motor programming influences programming time by itself. Exp Brain Res 2002; 144: 414–8.
15. Fisher RJ, Galea MP, Brown P, Lemon RN. Digital nerve anaesthesia decreases EMG-EMG coherence in a human precision grip task. Exp Brain Res 2002; 145: 207–14.
16. Wing AM, Flanagan JR, Richardson J. Anticipatory postural adjustments in stance and grip. Exp Brain Res 1997; 116: 122–30.
17. Wing AM. Posture and grip. In: Schöllhorn WI, Bohn C, Jäger JM, Schaper H, Alichman M eds. Book of abstratcs of European Workshop on Movement Science. Müster: University of Müster, 2003: 10.
18. Flanagan JR, Wing AM. Modulation of grip force with load force during cycling arm movements. Exp Brain Res 1995; 105: 455–64.
19. Flanagan JR, Wing AM. The role of internal models in motor learning and control: Evidence from grip force adjustments during movements of hand-held loads. J Neurosci 1997; 17: 1519–28.
20. Kazennikov O, Wicki U, Corboz M, Hyland B, Palmeri A, Rouiller EM, Wiesendanger M. Temporal structure of a bimanual goal-directed movement sequence in monkeys. Eur J Neurosci 1994; 6: 203–10.
21. Bootsma RJ, Marteniuk RG, MacKenzie CL, Zaal FT. The speed-accuracy trade-off in manual prehension: Effect of movement amplitude, object size and object width on kinematic characteristics. Exp Brain Res 1994; 98: 535–41.
22. Dubrowski A, Bock O, Carnahan H, Jüngling S. The coordination of hand transport and grasp formation during single- and double-perturbed human prehension movements. Exp Brain Res 2002; 145: 365–71.
23. Gentilucci M, Castiello U, Corradini ML, Scarpa M, Umilta C, Rizzolatti G. Influence of different types of grasping on the transport component of prehension movements. Neuropsychologia 1991; 29: 361–78.
24. Gentilucci M, Chieffi S, Scarpa M, Castiello U. Temporal coupling between transport and grasp components during prehension movements: Effects of visual perturbation. Behavior Brain Res 1992; 47: 71–82.
25. Jeannerod M, Decety J, Michel F. Impairment of grasping movements following a bilateral posterior parietal lesion. Neuropsychologia 1994; 32: 369–80.
26. Roland RE, Larsen B, Lassen NA, Skinhoj E. Supplementary motor area and other cortical areas in organization of voluntary movements in man. J Neurophysiol 1980; 43: 118–36.
27. Chen R, Hallett M. The time course of changes in motor cortex excitability associated with voluntary movement. Can J Neurol Sci 1999; 26: 163–9.
28. Alegre M, Labarga A, Gurtubay IG, Iriarte J, Malanda A, Artieda J. Movement-related changes in cortical oscillatory activity in ballistic, bustained and negative movements. Exp Brain Res 2003; 148: 17–25.
29. Ohara S, Ikeda A, Kunieda T, Yazawa S, Baba K, Nagamine T, Taki W, Hashimoto N, Mihara T, Shibasaki H. Movement-related change of electroencephalographic activity in human supplementary motor area proper. Brain 2000; 123: 1203–15.
30. Kasai T, Kawai S, Kawanishi M, Yahagi S. Evidence for facilitation of motor evoked potentials (MEPs) induced by motor imagery. Brain Res 1997; 744: 147–50.
31. Rossi S, Pasqualetti P, Tecchio F, Pauri F, Rossini PM. Corticospinal excitability modulation during mental simulation of wrist movements in human subjects. Neurosci Lett 1998; 243: 147–51.
32. Lemon RN. Functional properties of monkey motor cortex neurones receiving afferent input from the hand and fingers. J Physiol (Lond) 1981; 311: 497–519.
33. Picard N, Smith AM. Primary motor cortical activity related to weight and texture of a grasped object. J Neurophysiology 1993; 68: 1867–81.
34. Iberall T, Bingham G, Arbib MA. Opposition space as a structuring concept for the analysis of skilled hand movements. Exp Brain Res 1986; Suppl 15: 158–73.

35. Paulignan Y, MacKenzie C, Marteniuk R, Jeanerod M. Selective perturbations of visual input during prehension movements. 1. The effects of changing object position. Exp Brain Res 1991; 83: 502–12.

36. Johansson RS, Westling G. Signals in tactile afferents from the fingers eliciting adaptive motor responses during precision grip. Exp Brain Res 1987; 66: 141–54.

37. Johansson RS, Westling G. Programmed and reflex actions to rapid load changes during precision grip. Exp Brain Res 1988; 71: 59–71.

38. Johansson RS, Cole KJ. Grasp stability during manipulative actions. Can J Physiol Pharmacol 1994; 72: 511–24.

39. Wannier TMJ Maier MA, Hepp-Reymond MC. Contrasting properties of monkey somatosensory and motor cortex neurons activated during the control of force in precision grip. J Neurophysiol 1991; 65: 572–89.

40. Porter R, Lemon RN. Corticospinal neurones and voluntary movement. Oxford: Oxford University Press, 1993: 428. In: Lemon, Johansson, Westling. Corticospinal control during reach, grasp, and precision lift in man. J Neurosci 1995; 15: 6145–56.

41. Day BL, Riescher H, Stuppler A, Rothwell JC, Marsden CD. Changes in the response to magnetic and electrical stimulation of the motor cortex following muscle stretch in man. J Physiol (Lond) 1991; 433: 41–57.

42. Palmer E, Ashby P. Evidence that the long latency stretch reflex in humans is transcortical. J Physiol (Lond) 1992; 449: 429–40.

43. Barker SBN, Olivier E, Lemon RN. Recording the pyramidal volley evoked by transcranial magnetic stimulation in a coscious monkey. Exp Brain Res 1994; 99: 529–33.

44. Flament D, Goldsmith P, Buckley CJ, Lemon RN. Task dependence of responses in first dorsal interosseous muscle to magnetic brain stimulation in man. J Physiol (Lond) 1993; 464: 361–78.

45. Lemon RN, Johansson RS, Westling G. Corticospinal control during reach, grasp, and precision lift in man. J Neurosci 1995; 15: 6145–56.

46. Westling G, Johansson RS. Responses in glabrous skin mechanoreceptors during precision grip in humans. Exp Brain Res 1987; 66: 128–40.

47. Johansson RS, Macefield G, Häger C. Signals in cutaneous afferents triggering grip force responses during restraint of an object held by finger and thumb. Eur J Neurosci 1991; suppl 4: 2072.

48. Johansson RS, Häger C, Bäckström L. Somatosensory control of precision grip during unpredictable pulling loads. III. Impairments during Digital Anaesthesia. Exp Brain Res 1992; 89: 204–13.

49. Jeanerod M, Arbib MA, Rizzolatti G, Sakata H. Grasping objects: The cortical mechanisms of visuomotor transformation. Trends Neurosci 1995; 18: 314–20.

50. Oxford Dictionary of Scientists. Oxford: Oxford University Press, 1999: 5, 351.

51. Vallbo AB, Hagbarth KE, Torebjörk HE, Wallin BG. Somatosensory, proprioceptive and sympathetic activity in human peripheral nerves. Phys Rev 1979; 59: 919–57.

52. McKloskey DI. Kinesthetic sensibility. Phys Rev 1978; 58: 763–820.

53. Gandevia SC. Kinesthesia: Roles of afferent signals and motor commands. In: Rothwell I, Sheperd JT eds. Handbook of physiology. New York: American Physiological Society, 1996: 128.

54. Kandel ER, Schwartz JH, Jessel TM. Principles of neural science. New York: McGraw-Hill, 2000: 430–50.

55. Chapman CE, Tremblay F, Ageranioti-Belanger S. Role of primary somatosensory cortex in active and passive touch. In: Wing AM, Haggard P, Flanagan JR eds. Hand and Brain: The neurophysiology and psychology of hand movements. San Diego: Academic Press, 1996: 329–47.

56. Claus D, Mills KR, Murray NM. Interaction of transcranial magnetic stimulation and mechanical stimuli. EEG EMG Z Elektroenzephalogr Elektromyogr Verwandte Geb 1988; 19: 222–7.

57. Aimonetti JM, Nielsen JB. Changes in intracortical excitability induced by stimulation of wrist afferents in man. J Physiol 2001; 534: 891–902.

58. Aimonetti JM, Vedel JP, Schmied A, Pagni S. Inhibition versus facilitation of the reflex responsiveness of identified wrist extensor motor units by antagonist flexor afferent inputs in humans. Exp Brain Res 2000; 133: 391–401.

59. Deletis V, Schild JH, Beric A, Dimitrijevic MR. Facilitation of motor evoked potentials by somatosensory afferent stimulation. Electroenceph Clin Neurophysiol 1992; 85: 302–10.

60. Hirashima F, Yokota T. Influence of peripheral nerve stimulation on human motor cortical excitability in patients with ventrolateral thalamic lesion. Arch Neurol 1997; 54: 619–24.

61. Clouston PD, Kiers L, Menkes D, Sander H, Chiappa K, Cros D. Modulation of motor activity by cutaneous input: inhibition of the magnetic motor evoked potential by digital electrical stimulation. Electroenceph Clin Neurophysiol 1995; 97: 114–25.

62. Inghilleri M, Berardelli A, Cruccu G, Manfredi M, Priori A, Rothwell JC. Inhibition of hand muscle motoneurons by peripheral nerve stimulation in the relaxed human subject. Antidromic versus orthodromic input. Electroenceph Clin Neurophysiol 1995; 97: 63–8.

63. Abbruzzese G, Marchese R, Buccolieri A, Gasparetto B, Trompetto C. Abnormalities of sensorimotor integration in focal dystonia. A transcranial magnetic stimulation study. Brain 2001; 124: 537–45.

64. Tokimura H, Di Lazzaro V, Tokimura Y, Oliviero A, Profice P, Insola A, Mazzone P, Tonali P, Corthwell JC. Short latency inhibition of human hand motor cortex by somatosensory input from the hand. J Physiology 1999; 523: 503–13.

65. Dimitrijevic MM. Mesh-glove. 1. A method for whole-hand electrical stimulation in upper motor neuron dysfunction. Scand J Rehab Med 1994; 26: 183–6.

66. Dimitrijevic MM, Soroker N. Mesh-Glove. 2. Modulation of residual upper limb motor control after stroke with whole-hand electric wtimulation. Scan J Rehab Med 1994; 26: 187–90.

67. Dimitrijevic MM, Stokic DS, Wawro AW, Wun CC. Modification of motor control of wrist extension by mesh-glove electrical afferent stimulation in stroke patients. Arch Phys Med Rehab 1996; 77: 252–8.

68. Sarabon N, Dimitrijevic MM, Zidar J, Mihelin M, Dimitrijevic MR. Temporal summation of afferent input bellow the level of sensory perception can induce modification of motor cortex excitability. In: Gantchev N ed. Proceedings of the from basic motor control to functional recovery III. Sofia: St. Kliment Ohridski University Press, 2003: 954–7.

69. Sarabon N, Dimitrijevic MM, Zidar J, Mihelin M, Dimitrijevic MR. Modification of muscle responses to transcranial magnetic stimulation (TMS) of motor cortex induced by peripheral afferents in humans. In: Lestienne FG, Denise P, Dufosse M, Latash ML, Levin MF, Thullier F eds. Progress in motor control IV. Caen: University of Caen, 2003: 147–8.

70. McManus C. Right hand, left hand: The origins and asymmetry in brains, bodies, atoms and cultures. London: Weidenfeld & Nicolson, 2002: 218.