

Motor learning, the contribution of afferent signals.

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Ladies and gentlemen,

In the first place I thank the organizers for the invitation to give a contribution to this conference.

My task is to give a general introduction in the neurophysiological aspects of moving in water, in order to give you that basic information necessary to follow with sufficient effect the lectures of the speakers of this day.

Since the audience consists partly of therapists and partly of medical practitioners, it is not easy to choose the level on which my talk has to start. If parts of my lecture for some of you are very well known, I hope you will forgive me my simplicity.

Movement is the consequence of the activity of muscles attached to parts of the skeletal bones. Movements are possible since bones articulate in a special way in the various joints.

Skeletal muscles do not contract of their own. They always need to be stimulated by impulses from the central nervous system.

One can distinguish two goals. Firstly, to give the muscles that tension to counteract the forces that disturb the posture of the body, at least when moving on land. In this respect the most important force is that of gravity. Secondly, to cause the movements of the body or parts of the body in the environment, whether it is in air or in water.

This two-fold function of the muscles require two types of muscle fibres. To maintain posture, muscle fibres must be able to be in contraction for a long period without getting fatigued. Movements on the other hand require muscle fibres that can contract very fast and with a great force.

In man, most muscles are mixed; that means that they consist of so-called "slow twitch muscle fibres" as well as of "fast twitch muscle fibres". It is interesting to know that, it depends on its innervation whether a muscle fibre during development will become slow or fast. There are various theories to explain this. One of the most attractive is that, when a muscle fibre is continuously stimulated with a low frequency, it will become "slow", and when it is stimulated only from time to time with a high frequency it will become "fast". This has been experimentally proved.

Muscle fibres are innervated in groups by only one motor nerve fibre. Stimulation of this motor fibre always induces a contraction of all the muscle fibres it innervates. Therefore, a motor nerve fibre and all the muscle fibres it innervates can

be considered as a functional unit, the so-called "motor unit".

The innervation of the muscle fibres is, as we may expect, also twofold. The slow type motor units have, with respect to the fast type, thinner nerve fibres, the α 2-fibres that conduct with a lower velocity.

The α 2-nerve cells in the spinal cord of the slow type motor units are relatively small and have a low threshold for stimulation. That means that they can easily be brought to activity. The nerve cells of the fast type motor units, the α 1-cells, are larger and have a high threshold, which means that they can only be activated by stronger stimulation.

Table 1 resumes the different qualities of both types of motor units.

	<u>slow type</u>	<u>fast type</u>
function	posture	movements
twitch	slow	fast
duration crescent/ decreascent (in humans)	45/50 ms (m. soleus)	18/20 ms (m. gastrocnemius)
tetanic fusion frequency	<30 ms	60-100 ms
motor units	small	large
motor nerve fibres	α 2-fibres (slower cond.)	α 1-fibres (fast cond.)
motor nerve cells	small low threshold	large high threshold
capillarisation	rich	less rich
myoglobin content	high	very low
energy production	aëroob	anaëroob/ aëroob
fatiguing	late	early

The central nervous system consists of an extremely complicated network of nerve cells with their offshooting nerve fibres. During evolution the morphologic structures, and the functional properties of the nervous system have grown tremendously. All these morphological and functional attainments are genetically tied up in the chromosomes of the cells.

Although the development of the nervous system in the embryonic stage is genetically determined it appears that all kinds of stimuli from the environment immediately after birth and in the very early childhood are of great importance for the future functional properties of the central nervous system.

Immediately after birth a lot of reflex pathways exist, some of which will be maintained during our whole life, others will only be used for a short time, for example the sucking reflex.

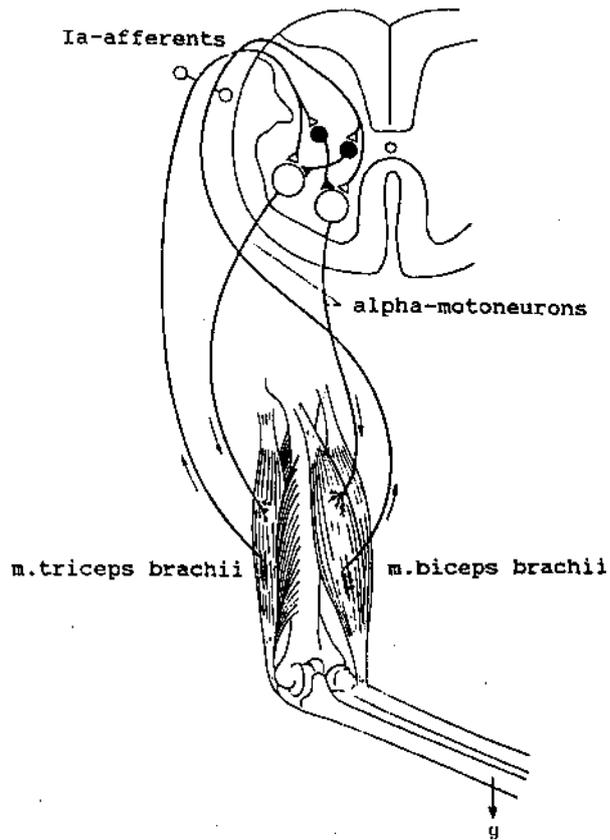


Figure 1.

Stretch reflex pathways for flexors and extensors in the upper arm. The black neurons are inhibiting interneurons. Weight g of the under arm tends to decrease flexion and to increase extension. However, flexortension is reflexly increased, and extensortension decreased.

One of the most important reflexes is the so-called stretch reflex. It forms the fundamental basis of the control of posture. It helps to counteract the external forces that may disturb posture. In evolution this reflex is first seen in the quadruped reptiles.

Posture would be disturbed when the length of the muscles that maintain posture is not controlled. However, muscles contain muscle spindles; they are sensors that are extremely sensitive to changes in length. They become active when they are stretched. Their discharge has a phasic and a tonic component. That means that a sudden stretch results in an acute discharge of high frequency (the phasic component), while a slow stretch results in an increase of frequency that is proportional to the quantity of stretch.

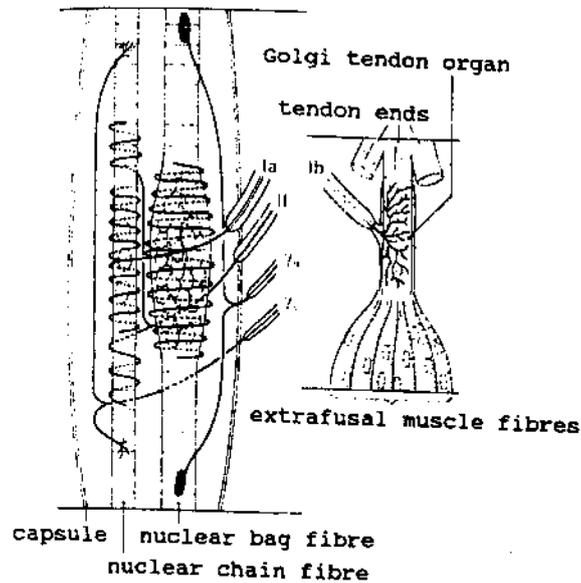


Figure 2.

Schematic drawing of the innervation of a muscle spindle and a Golgi tendon organ. Only the equatorial parts of one bag fibre and one chain fibre of the muscle spindle are given.

The muscle spindles contain, a general, a bundle of intrafusal fibres, which are in fact muscle fibres; halfway these fibres, for some part, they are not contractile. This part is surrounded by an annulo-spinal ending of a very fast conducting Ia-afferent nerve fibre. This part of the muscle spindle is the stretch sensitive part.

When awake the intrafusal fibres are continuously kept in contraction by the innervation of separate, so-called fusimotor fibres or gamma-fibres. That means that in the awake state the stretch sensitive part is slightly stimulated. An increase in length of the muscle spindle will enhance the basic discharge of the Ia-afferent nerve fibre.

The Ia-afferent nerve fibres monosynaptically facilitate the alpha-motoneurons of the same muscle and inhibit disynaptically the antagonistic muscles. Stretch of a muscle will thus result reflexly in a contraction of the same muscle. By this the external force that will disturb posture is counteracted by an opposite directed force from the muscle.

So it is clear, that the function of the stretch reflex is to counteract the external forces (f.i. gravity) that disturb the length of the muscles and thus give a fundamental contribution to the control of posture on land. When standing, muscle spindles prevent that we will fall. When walking, every moment that the sweeping leg becomes the standing leg, the stretching of the extensor muscles will call forward the stretch reflex to bear the weight of the body. When landing after a jump, the same extensor muscles of both legs catch the body weight.

It is obvious that, to make movements, muscles must be able to shorten or to lengthen. This may not be inhibited by the stretch reflex. The way in which nature has solved this problem is very easy. When a muscle shortens as a consequence of alpha-motoneurone stimulation the intrafusal motor fibres are stimulated simultaneously by the gamma- or fusimotor innervation, so that the muscle spindle shortens with the muscle. And the other way around: if a muscle lengthens by reduced alpha-motor stimulation, gamma-motor stimulation is reduced simultaneously, so that the muscle spindle lengthens with the muscle. This is a very important point of coordination and is called alpha-gamma linkage, or alpha-gamma coactivation.

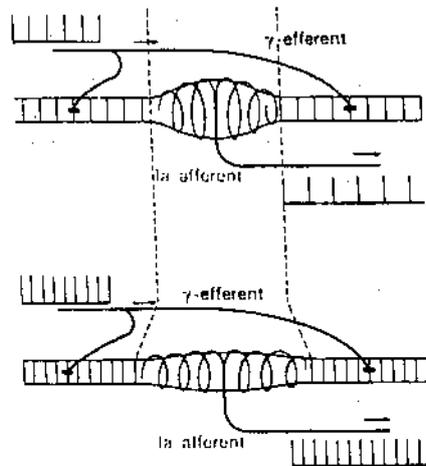


Figure 3.

Effect of stimulation of gamma motor neurons when both ends of the muscle spindle are fixed.

An interesting result of alpha-gamma coactivation is the so-called 'load compensating reflex'. If one tries to lift a weight, alpha- and gamma nerve fibres to those muscles that are responsible for the lifting manoeuvre are activated. In the first stage of action muscle fibres contract without shortening (isometric contraction). Intrafusal fibres contract also but the muscle spindle is prevented to shorten. Now the intrafusal fibres stretch the sensitive part of the sensor so that the Ia-afferent nerve fibre activity increases. This will strongly facilitate the alpha-motoneurons with which they synapt. So the stretch reflex helps to overcome the force of the weight that has to be lifted.

The same happens in water. If we try to make movements the shortening of the muscles is counteracted by the viscosity of the water. The load compensating reflex now assists in making the movements against the viscosity of the water. So far we have seen that by means of the stretch reflex exter-

nal forces that act upon the body can be caught by the stretch reflex. In this way the muscles act like springs. In technics we have springs of different sizes and stiffness in relation to the force they have to counteract. Our body has only one kind of springs: our muscles. Yet the stiffness of our muscles can be regulated. The sensitivity of the muscle spindle for stretch increases with increasing fusimotor stimulation. If, for example, we jump from a great height, during the gliding phase fusimotor activity increases, Ia-afferent activity increases, and by strong facilitation of alpha-motor-neurons muscle tone increases. So we land with the extensor muscles already in contraction (high stiffness of our springs). At the moment of landing, stretch reflex is strengthened by the increased sensitivity of the muscle spindles, so as to overcome the increased force of the landing body.

The tendon parts within the muscle also contain sense organs, sensitive to stretch (see figure 2.). The difference with the muscle spindles is that they lie in series with the muscle fibres, whereas the muscle spindles lie parallel to them. The consequence is that they are activated by passive lengthening (external force) and by active contraction of the muscle as well.

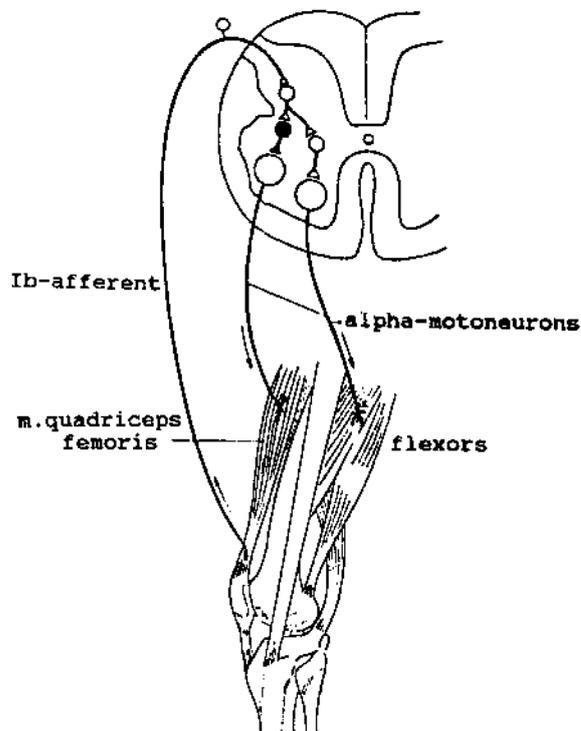


Figure 4.
Reflex pathway of the Golgi tendon reflex in muscles of the upper leg. The black neuron is an inhibiting interneuron.

They are connected with the spinal cord by thick, fast conducting Ib-fibres. By means of two interneurons they are connected with the alpha-motorneurons of the same muscle. The second interneuron inhibits the alpha-motorneuron, as can be demonstrated by artificial stimulation of the Ib-fibres and intracellular recording of alpha-motorneuron activity. Since reflex inhibition, as a result of stretching the muscle, has a high threshold one might think that the function of this reflex is only to prevent extreme contraction of the muscle, and thus to prevent damage to the tissue. We now think that the Golgi tendon organs, as these sensors are called, have an important function in the fine control of muscle tone. Since the tendon organs are stimulated by increasing tension in the muscle they contribute to the afferent information to the cerebral cortex about muscle tension.

This brings me to the point of the awareness of our motor activity. The most important stream of information that brings our motor activity to consciousness results from the activity of proprioception. That is the information from the muscle spindles, the tendon organs, the joint receptors, and the vestibular apparatus.

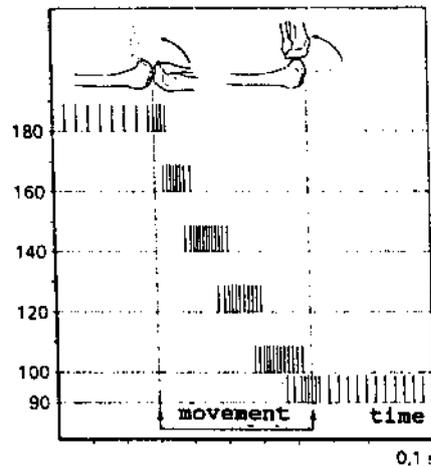


Figure 5.

Schematic drawing of the stimulation of joint receptors before, during and after a movement. The vertical axis gives the rotation in grades.

As the tendon organs give information about muscle tension it is the activity of the joint sensors that gives the most important contribution to the awareness of our movements. Joint sensors can give static information about posture as well as phasic information about the speed of movement. By this, one can be continuously aware of the place of any part of the motor apparatus in relation to the whole body and to the environment.

Exteroceptive information from the skin, overlying the joints mildly contributes to the awareness of movements in air. In

water, however, the continuous contact and friction between the skin and the medium increases exteroceptive information considerably. As we may expect this will contribute to the awareness of our motor activity.

Besides the information from the skin the most important exteroceptive information for motor activity is given by vision. With our eyes we have a continuous information of the relation between our moving body and the environment. We all know the hesitating gait of a blind person, and we can experience it ourselves by walking and moving with closed eyes. A blind patient in the water will have undoubtedly an extra handicap in motor function by lack of vision. On the other hand as a consequence of functional plasticity of the brain, he makes much more and discriminative use of all tactile information, even of the auditive stimuli from the environment.

Up to now we concentrated on the peripheral part of the nervous system in relation with the spinal cord, and to some extent on the afferent information to the cerebral cortex. How important the reflex function of the spinal cord in relation to posture and movement is, a contemplation of motor control on spinal level alone is much too simple. It is known from experimental research, that most of the reflex activity of the spinal cord is under control of centres on a supraspinal level. From the classic decerebration experiments of Sherrington f.i. we know that the control of extensor tone in the limbs of most quadruped mammalians is under control of centres in the reticular formation in the brain stem.

Cools in his contribution will deal with the contribution of supraspinal structures on movement in water.

The last point I will deal with is the contribution of afferent signals to motor learning, as has been mentioned in the title.

The importance of afferent signals for motor activity has been demonstrated in an experiment with a monkey of which the dorsal roots of one arm were cut. After the operation the monkey behaved as if it had only 3 extremities. It did not use the de-afferented arm any more, although the motor-innervation had remained intact. Obviously the animal was not aware of having that arm.

Like a deaf child does not learn to speak, motor learning is impossible without feedback by means of proprioceptive and exteroceptive information.

Our knowledge of the neurophysiological events in motor learning is still very fragmentary.

In motor learning force, and/or velocity, direction and measure of movements have to be coordinated by activating a well chosen number of motor units during sufficient time.

The initiation of movements starts in the cerebral cortex.

Impulses reach the α -motorneurons by the pyramidal and gradually also more and more by the extrapyramidal connections. The coactivation of gamma-fibres prevents the counteraction of the stretch reflex. When motor activity takes place, by feedback

information from proprioception, vision, and in water from exteroceptive information from the skin, we become aware of our movements. This comes to consciousness in the postgyral areas of the brain, mainly in area 7. So we have a memory of our movements.

Feedback information from the motor apparatus runs also to the cerebellum which is informed from the cerebral cortex about the movement that has to be fulfilled via cortico-ponto-cerebellar connections: So the cerebellum can contribute to coordination of movements. Repetition of the movement will gradually lead to programming of this movement in premotor areas of the cerebral cortex.

As I have tried to make clear, the sensory feedback to the cerebral cortex is indispensable for motor learning. If, by any pathologic process, proprioceptive feedback is impaired, exteroceptive feedback from movement in water can be of inestimable value for motor learning processes.

Because sensory information is extremely important for motor-activity it is incorrect to speak of "the motor system". We have to deal with "the sensory motor system".