

SYNAPTIC PLASTICITY AND MOTOR LEARNING

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ABSTRACT

The volume and ability of processing information by the human brain depends not on the number of neurons but on the number of synaptic connections between them. The neural networks in the brain develop during one's lifetime. Their development is affected by genetic and environmental factors as well as by acquired experiences. The plasticity of the healthy brain refers to a re-organization of the cortex in response to learning and experience. The key sites responsible for the creation and decay of brain plasticity are synapses. A synapse constantly modifies its properties affecting the efficiency of neurotransmission. This unique ability of synapses is known as synaptic plasticity and is regarded as the cellular foundation of learning and memory. The number of synapses and dendrites of cortical neurons increases when motor learning occurs with a simultaneous influence of environmental stimuli. Considering the significance of synapses in the learning process it can be stated that memories and experiences are not stored in the brain matter but in the inter-matter spaces (Douglas Fields 2009). Training and experience augment the cortical representation of exercised motor functions (Kinalski 2008).

Key words: engram, synaptic augmentation, long-term potentiation (LTP), metaplasticity

INTRODUCTION

The volume and ability of processing information by the human brain depends not on the number of neurons but on the number of synaptic connections between them. The neural networks in the brain develop during one's lifetime. Their development is affected by genetic and environmental factors as well as by acquired experiences. The plasticity of the healthy brain refers to a re-organization of the cortex in response to learning and experience. The key sites responsible for the creation and decay of brain plasticity are synapses. A synapse constantly modifies its properties affecting the efficiency of neurotransmission. This unique ability of synapses is known as synaptic plasticity and is regarded as the cellular foundation of learning and memory. The number of synapses and dendrites of cortical neurons increases when motor learning occurs with a simultaneous influence of environmental stimuli. Considering the significance of synapses in the learning process it can be stated that memories and experiences are not stored in the brain matter but in the inter-matter spaces. Training and experience augment the cortical representation of exercised motor functions (Kinalski 2008).

The brain of an adult consists of about 100 billion neurons, each of which forming on average about 1,000 synapses which connect it with other neurons.

The precursors of the concept of synaptic augmentation in the learning process were Konorski (1948). He claimed the existence of inactive potential connections between neurons and groups of neurons that were formed during the ontogenesis, which under specific circumstances could become activated. During learning, when the stimulation of the transmitting neuron co-occurs repeatedly with the stimulation of the receiving neuron, the synapses become increasingly activated at the meeting point between the axon terminals of the two neurons. This enhanced activity can be related to morphological and/or biochemical changes in the synapses.

The development of bioengineering and computer data analysis has allowed present-day clinical neurophysiologists to verify the hypotheses from the middle of the 20th century. The experimental neurophysiologists, who had developed the earlier models of plasticity and regeneration of the central nervous system in adolescents and adults, often accurately, however intuitively described the neural processes in humans and animals. The concept of long-term potentiation (LTP) was introduced (Sadowski 2008), which confirmed the phenomenon of long-lasting synaptic enhancement. LTP shows how synaptic connections can change due to neural activity (Kossut 2005). It is one of the most frequently studied models of cellular changes of synaptic plasticity. A high-frequency stimulation of axons in the brain induces the LTP of postsynaptic neurons. LTP was first discovered in the hippocampus, i.e. in the human brain component responsible for learning and consolidation of information from short-term memory to long-term memory (Malenka and Nicoll 1999).

The opposite process to LTP is long-term depression (LTD). A repeated stimulation of certain neural pathways may lead to another form of plasticity, i.e. a long-lasting reduction in the efficacy of neuronal synapses. This process is regarded as a typical example of neuroplasticity during the development of motor skills in which learning involves constant adjustments of erroneous motor behaviors (Gut 2007). Long-term depression enables the suppression of undesired motor habits in the learning process as well as the development of motor skills useful at work and in sport.

FROM MOTOR LEARNING TO NEUROPLASTICITY

Schmidt's theory of motor programs (1991) is one of the most useful concepts of organization of human motor activities. It is exemplified by the model of psychomotor response, which in its processing part involves three stages: identification of stimuli, choice of a sensory-motor response and programming of the response. Once the processing of stimuli is completed a specific motor program is launched which then in the form of an electrical impulse reaches the muscle via the spinal cord and initiates a movement.

Evidence for the concept of motor programs includes the following:

- reaction time is always longer in complex movements;
- animals surgically deprived of sensory information are able to perform relatively efficient movements;
- patterns of muscle activity remain the same for the first 100-120 ms, and movement is possible even without feedback from the moving limb.

In the late 1980s the concept of motor programs was elevated to the rank of scientific theory and was described by Schmidt in his momentous work *Motor Control and Learning* (1988). The main tenets of the theory were abstract. Information processing cannot be seen with the naked eye. Only an external outcome can be seen in the form of a concrete physical activity. Internal processes are hypothetical and cannot be directly observed. The knowledge of them is still an open source and it allows drawing various conclusions on causes of human behaviors in experimental conditions.

For decades it was impossible to directly observe the neural processes and their precise location in the brain. However, the most recent technological developments (MRI, PET, confocal microscopy) enabled direct tracking of effects of experiences and motor learning in the neural system. It can be assumed that the newest technological advancements will "add luster" to the Motor Control theory and empirically justify its main assumptions.

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Muscles contract in response to commands sent by the axons on motor neurons to the synapses on muscles known as neuromuscular connections. When an axon generates an electrical impulse the synaptic vesicles release a chemical neurotransmitter called acetylcholine, which then excites the neurotransmitter receptors on the muscle fiber inducing a contraction. The communication

in a neuromuscular connection is similar to the communication in any other synapse between two neurons in the brain. The postsynaptic neuron generates an electrical impulse in response to a signal from the synapse in the same way as a muscle fibre. The electrical energy then spreads in the entire muscle cell invoking a contraction.

Neurons are the longest cells in the human body. For example, the motor neuron between the spinal cord and the hallux is about 1 m long. The speed of neurotransmission amounts to 320 km per hour. In synapses the impulse slows down to about 4 ms. The structure of many sensori-motor reflexes of defensive character involves only one synapse in the spinal cord between the sensory and the motor neuron invoking the reaction of the muscle. The well-known patellar reflex or knee-jerk is very rapid, one may say, mono-synaptic. It is after the execution of a movement, certainly unconsciously, that other nerves send information to the brain about the quality of execution of a given reflex. Reflexes constitute the neurobiological foundation of the entire human motor function based, however, on more complex neural feedback networks involving the motor cortex, the cerebellum and brain structures responsible for motor memory.

Motor learning is not only the plasticity of synapses that enables modifications of functional connections due to experiences. It is subject to more subtle regulation than the creation of new synapses and destruction of the old ones. Through releasing more neurotransmitter from the presynaptic terminal after the arrival of an impulse, or through a change in the sensitivity of the postsynaptic neuron, the charge in the synapse may induce smaller or bigger changes in the charge in the postsynaptic neuron and thus weaken or strengthen the neural connection. In other words, synapses can be likened to checkpoints controlling the flow of information in neural networks. The synaptic control of information flow enables the strengthening or weakening individual networks in response to experiences or learning. In such a case synapses play a functional role. The creation of new synapses is a long-lasting, complex process and pertains to much more complex motor activities.

Nerve cells that discharge at the same time become connected. The temporal coordination of their functional potentials is highly significant for determination which synaptic connections should be strengthened and retained, and which should be weakened and eliminated. A very similar process of axonal re-organization occurs when the neurons in the spinal cord connect to particular muscles. In adults each muscle fiber is connected only to one motor neuron. However, at the beginning, when neurons make their first contact with muscle fibers, each muscle fiber receives connections from many motor neurons. Then some neuromuscular connections are eliminated until the final pattern of connections is established. This elimination process requires specific time patterns of the activity of functional potentials generated by motor neurons.

Overlearning

Synaptic plasticity performs yet another highly significant function in the brain: it aids damaged brain recovery. If neurons that control some specific movements become destroyed, for example, after a stroke or severe head injury, not everything becomes necessarily destroyed. In most cases nerve cells do not re-grow. Instead other neurons adapt and with time take over functional roles similar to those of the lost neurons, and form other but similar networks. This process, called overlearning, stresses some convalescent capabilities of the brain. It should be remembered, however, that this plasticity is temporary, e.g. it can be observed after training but then returns to the original state (Kusnierz 2007).

It is commonly believed that the growth of new synapses lasts much longer and thus occurs later. For example, when a trained task becomes overlearned or automated, new connections responsible for its execution are strengthened. Thus variable and short-term modifications of the existing connections constitute the first and necessary stage leading to a permanent re-structuring in the cortical and subcortical networks. The phenomenon of overlearning is in fact the essence of development of motor habits. It is especially important for learning techniques in various sports and for development of motor skills in individual athletes. Along the development of athletes' energetic potential individual skill levels should be developed through perfecting motor programs in order to be able to face new requirements. Some old motor habits should be overlearned while other should be raised to the level of motor automatisms required from elite competitors.

The "unmasking" effect

Certainly, short-term training does not enable the development of entirely new synaptic connections. There is, however, an alternative way to activate dormant (inactive) synapses in response to non-typical environmental stimulation, e.g. vision loss or sensory deprivation. The human brain contains a number of potential neural connections which in a normal situation (before a surgery, training, etc.) do not play any significant role, do not function – in other words – remain "masked". These are, for example, inactive points of entry to sensory areas from regions controlling a different sensory modality. A specific external stimulus can reveal their potential and cause, for example, the visual cortex to assume the function of processing signals from other sensory modalities. This process is often referred to as the "unmasking" effect, thanks to which "masked" connections become activated in response to environmental stimulation and function as long as they can fulfill their tasks effectively (Hess Donoghue 1994).

The aforementioned authors claim that maps of certain areas show connections which are normally subliminal and do not reveal their roles. They have a certain potential, which is revealed once a typical signal of a connection from the dominant map is for some reasons removed. Therefore, if the main connection to a specific cortex area is damaged, and consistently, the dominant afferent neurons are inhibited, weaker connections may be activated. Normally, such weaker connections are inhibited by stronger connections, however, this inhibition ceases once the latter are eliminated. This process does not exclude the possibility of creation of new axon projections, especially, in cases of long-lasting denervation. This can be observed when an intact axon neighbors on areas to which the flow of information has been inhibited. In this case active neurons project axon collaterals towards those less excited areas. Permanent changes in the functional organization of the central nervous system and long-lasting re-organization of the cortex are usually attributed to anatomic changes. This however does not diminish the significance of effectiveness of synapses responsible for this type of plasticity. Morphological studies have shown the growth and branching of axons and dendrites within partially denerved or de-activated areas of the somatosensory system (Buonomano, Merzenich 1998).

Neuroplasticity can result from the already existing "potential" of the brain, i.e. from stimulation of existing but hitherto unused neural connections. This phenomenon is well-known in sports, mostly in complex technical disciplines and in those involving constant rivalry with the opponent. Athletes and martial arts practitioners may often, in the heat of contest, use unexpected techniques which they have not trained for months, and which have remained "dormant" in their memory for a long time. On the other hand, in many competitions, e.g. in tennis, players may – on the spur of the moment, in an almost equilibristic manner – return balls and score points in the ways they have never trained at all. This happens only in the case of most talented players equipped with a vast array of motor experiences aimed at a given type of motor function. Unexpected tactical situations may release in those players an adaptive motor potential than can be effectively used in moments critical to winning a sport competition.

Learning and emotional states

The quality of our learning depends to a large degree on our emotional state. We have the tendency to "retain" in memory events that were particularly joyful, sad or painful. We also learn better, when we pay attention. Emotional states are linked to the release of neurotransmitters such as acetylcholine (during concentrated attention), dopamine, noradrenaline and steroid hormones, including cortisol (while experiencing the unknown, stress and anxiety). The modulators affect neurons in many different ways. Some of them act by altering the functioning of NMDA receptors. Their other activities include the activation of genes specifically related to learning. The proteins encoded by these genes help stabilize and prolong LTP.

Neurophysiological changes in synapses have their equivalent in psychological conditions and certainly affect each other. The two Yerkes-Dodson laws must be recalled here. The first law pertains to motor learning effectiveness based on the level of arousal of the nervous system. The other law is concerned with learning effectiveness with regard to types of motor tasks. In the first law the efficiency of learning of motor habits depends on an optimal state of arousal, i.e. endurance of the nervous system. A disturbance of this optimality results in a decrease in learning effectiveness. In the case of learners with high strength of nervous processes, a low level of arousal will not guarantee the effectiveness of learning new motor techniques. On the other hand, in sensitive learners with low stress resistance, excessively high arousal will result in low effectiveness of learning new motor habits. According to the second Yerkes-Dodson law, simple cyclical motor habits in activities based on speed and strength predispositions, should be learnt in conditions of high arousal; whereas complex motor habits should be acquired in conditions of low arousal. Studies of efficiency of elite athletes in technical sports show that excessive arousal, reflected by high levels of adrenaline and cortisol, lead to worse performance during competitions and defeats in combat sports or martial arts. In such cases these disturbances are psychologically interpreted as being associated with perturbations in synaptic transmission due to an excessive release of neurotransmitters.

CONCLUSION

1. Neuroplasticity is not only associated with engram structures in the central nervous system, but also with the peripheral nervous system at the spinal cord level in connections between axons and muscles and neural branchings in muscles themselves. From the standpoint of motor learning we deal here with the concept of metaplasticity of the neuromuscular system.
2. Muscles contract in response to signals sent by the axons of motor neurons to a synapse in the muscle known as a neuromuscular connection. Bioelectrical activity spreads in many nerve fibers, and it is of selective character in the case of well-mastered movements. Those muscles are stimulated with appropriate strength that ensures the fastest and most precise movement execution. The bioelectrical activity of the total of motor units measured with EMG is lower in performing retained movements as compared with new movements or newly learnt movements.
3. The mechanisms of learning new motor activities and perfecting acquired ones consist of removing weaker neural structures through the potentiation of trained synaptic connections. This process requires a specific activity of functional potentials of specific motor neurons. The desired neural networks and thus the ultimate motor patterns are formed in result of bioelectrical discharges at the right time. This particular timing ensures the retention of synaptic connections. It is not a permanent process. New experiences may yield new modifications and re-organizations of neural connections.
4. The multitude of motor experiences contributes to the formation of many neural pathways that constitute the motor supplies in humans from childhood until adulthood. Some of these pathways can be dormant and only supraliminal stimulation can activate their potential. As EMG analysis shows, a number of motor patterns in different professions, including sports, become automated under proper training, and such automatisms can be retained throughout the entire ontogenesis of human motor function. These automated patterns are uniquely accurate, rational and economical. It can be assumed that such neural connections are not only functional but strictly morphological.

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