Chapter 25

Motor learning

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Introduction

Learning is a process that refers to changes in behavior and in the central nervous system. Motor learning is defined as: 'a change in the capability of a person to perform a skill that must be inferred from a relatively permanent improvement in performance as a result of practice or experience' (Magill and Anderson, 2007). Motor learning covers three main types of learning procedure; 1) acquisition of a novel motor skill (novel task learning), 2) enhancement of performance of a learned or highly experienced motor skill (expertise), and 3) reacquisition of skills that are difficult to perform or cannot be performed because of injury, disorder or disease (rehabilitation). In order to understand motor learning, it is important to clarify the interrelated terms of motor skill and motor performance. Motor skill refers to a goal-directed activity or task that requires voluntary control over movements of the joints and body segments, whereas motor performance refers to the execution of a skill at a specific time and in a specific situation. Motor performance is an observable behavior, whereas motor learning cannot be observed directly, but rather, can be inferred from performance. Fig. 25.1A and B show the performance of rock climbing skill by professional athletes. Learning of this sport skill starts with observing and imitating an experienced climber. The novice climber closely monitors an experienced climber while experienced climber is ascending. In doing so, the novice might plan some explicit strategies such as, the rock edges for gripping with hands and feet. When attempting climbing, the novice must rely on sensory feedback from proprioceptive and tactile, vestibular, and visual organs for maintaining balance and movement control. In addition, trainers usually give explicit guidance, such as the direction of the next handling, or where to step. Despite all the explicit knowledge gathered by the novice, the practice relies on implicit musculoskeletal and neural processes. As in this example, motor learning and other sensory-perceptual and cognitive learning types often interact to achieve a skilled performance.

Learning hypotheses

Schmidt's schema theory of discrete motor skill learning was originally presented in 1974 at a meeting of the North American Society for Psychology of Sport and Physical Activity (Schmidt, 1975). According to the model, there is a generalized motor program, a schema, for a group of motor tasks. During learning of a motor skill, there are four important parameters to store in working memory. These are; 1) the conditions at the beginning of the movement, i.e. proprioceptive information about the posture, weight of a tool or object that is used, 2) the specifications for the motor program such as, speed and force, 3) the knowledge of results, or actual outcome, and 4) the sensory consequences of the movement response, how the movement felt, looked and sounded. These parameters compose the motor response schema. Important point is that the schema is modified in every execution of the movement based on the sensory feedback and knowledge of results. Schema model involves learning a recognition schema that is an error detection mechanism, and learning a recall schema that is the selection of accurate motor program.

Ecological theory of motor learning has been proposed recently by Newell (Newell, 1991). This model relies on perception-action coupling, and defines that optimal movement strategies are developed in the most efficient way given certain environmental constraints. Perception is important because the person needs to understand the goal of the task, learn the movement and interpret the feedback, both during and after the movement. In this approach, the model highlights the structural and functional constraints related to the individual, task, and environment, and views motor skill as a dynamic exploratory activity in perceptual-motor workspace.

FIGURE 25.1   Rock climbing is an exciting and challenging sport. During learning of rock climbing, beginners practice handling and stepping techniques, which exert pushing, pulling and compression forces to transfer body's center of gravity. Beginners start with low grade top rope climbing or bouldering routes that are easy therefore, more convenient for practising. In photos of rock climbing, performance of two Turkish National sport climbing athletes Duru Güneş Yalçın in 'Kısa Samsun' route (Grade 6c +) (A) and Zorbey Aktuyun during a lead climbing in 'Nessuono' route (Grade 8a + , 27 hours climbing) (B) are shown. Nessuono is a much more difficult route because of the structure of the rock that can be handled only by pinch gripping beyond endurance for 27 hours of climbing (B). Performance at the expert level has an endurance of finer movements and coordinative structure in handling and stepping techniques that are acquired as a result of extensive practice.
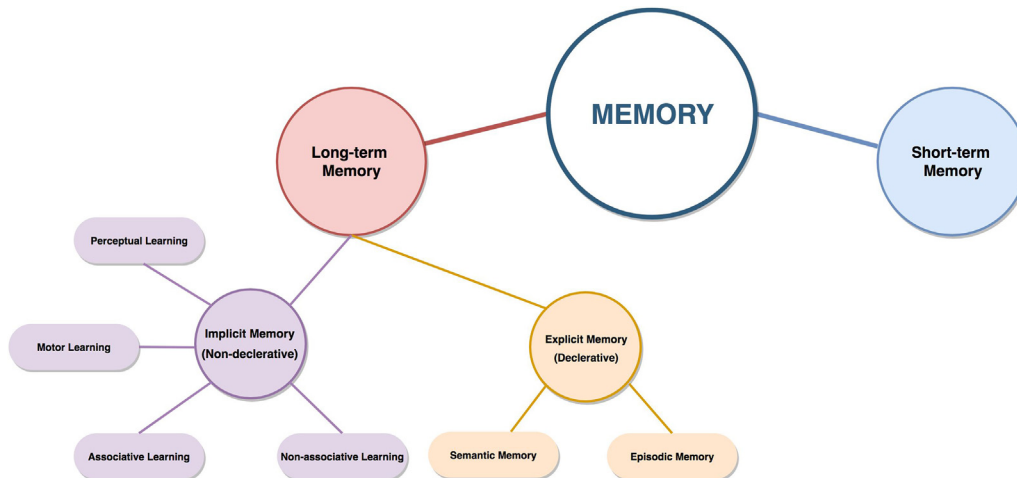

FIGURE 25.2   Classification of long-term memory and different systems of learning are presented. There is an interaction between learning and memory processes. Systems are not fully independent from each other, rather they depend on each other to some extent.

Behavioral approach

Learning and memory are both theoretical constructs, which are interconnected and inferred from behavior (performance). Learning is defined as 'an enduring change in the neural mechanisms of behavior that result from experience with environmental events' (Domjan and Burkhard, 1982). We can divide learning processes into two major types; implicit and explicit. Implicit learning defines an unconscious, yet extremely important process of learning that cannot be described verbally, unlike explicit learning, defined as the conscious process of learning facts, information, and events (Byrne, 1997). Regarding the wider theoretical framework of human learning, 'motor learning' is largely considered as an implicit learning process, and is used interchangeably with the term 'procedural learning'. Fig. 25.2 shows different types of learning and memory, and the place of 'motor learning' in this framework.

Below is the description of different learning types.

Perceptual learning

This refers learning perceptual skills, such as differentiating two colors, or the identification of different food tastes. Examples can be expanded for other sensory modalities; auditory, tactile, olfactory, and proprioception. Perceptual learning can be viewed as an essential part of complex cognitive functions. For example, being able to discriminate close sounds is a clear advantage in language learning (Ward, 2015). Similarly for motor learning, extracting and discriminating relevant sensory information is essential (Wolpert and Flanagan, 2010). Experienced soccer players showed advanced visual discrimination of an opponent's postural orientation, which enables them to anticipate their next movement (Williams, 2009), and to find relevant sensory information more quickly (van Maarseveen et al., 2015).

Associative learning

Associative learning modifies the behavior via relating one stimulus with another, or relating a stimulus with a particular behavior. In classical conditioning, a person pairs two stimuli, and therefore reflex response is modified. In operant conditioning, a person pairs his/her own behavior with the consequences of that behavior (Kandel et al., 2000). *Classical conditioning* is a simple form of associative learning, where the behavioral response is modified by conditioned stimulus. In the classical example, developed by Ivan Pavlov, dogs produce reflex response of salivation when conditioned with a sound stimulus. In the experiment, dogs associated the sound stimulus with the food (natural stimulus leading to salivation response) after sufficient conditioning. Then, the dog shows salivation response to the sound in the absence of food. Classical conditioning is usually related to 1) emotional responses and 2) skeletal muscle responses. Eye blink conditioning is a form of classical conditioning that has been studied in the investigation of neural mechanisms underlying learning and memory. A mild air puff is a natural stimulus that results in an eye blink reflex. In the experiment, the air puff is paired with visual or auditory stimuli, so that, for example, eye blink reflex is seen when a person hears a sound. The eye blink conditioning experiments showed the important role of cerebellum in associative learning; especially in acquisition and timing of motor actions (Gerwig et al., 2007).

Operant conditioning (also called trial-and-error learning) is another type of associative learning in which a voluntary motor behavior is strengthened or weakened, depending on its favorable or unfavorable consequences. When motor behavior is associated with desirable consequences such as a reward (positive reinforcement), there is a tendency to repeat the behavior. In the opposite situation, when the behavior results in unwanted consequences, such as pain or failure (negative reinforcement), it will decrease the likelihood of its occurrence. In rehabilitation science, operant conditioning of spinal reflex has been investigated as a promising tool for locomotion. Simply stated, stimulus-induced muscle responses (reflexes) are used to induce neuroplasticity. In a study by Wolpaw's group, patients with incomplete spinal cord injury decreased H-reflex of soleus muscle with operant down-conditioning, which was associated with faster and more symmetrical locomotion (Thompson et al., 2013). Similarly, operant up-conditioning has been led to increase in motor-evoked potential of tibialis anterior in incomplete spinal cord injury (Thompson et al., 2018).

Nonassociative learning

Nonassociative learning involves learning the properties of a single stimulus. Simple forms of *non-associative learning* consists of habituation and sensitization. Habituation refers to diminishing response amplitude, while sensitization refers to increasing response amplitude to the repeated stimulus (Kandel et al., 2000). Habituation is important for minimizing the energy expenditure of the motor system. Studies have shown that large automatic responses to unexpected movements of a supporting platform are progressively decreased due to a generalized habituation in the postural control system (Keshner et al., 1987). Similar postural control responses occur very frequently in everyday life, for example, while standing in a moving bus, sudden braking results in larger postural reactions at first, but subsequent similar braking results in less dramatic postural reactions. In addition, habituation may be an important factor to consider in orthopedic injuries. Stretch reflex response of the lateral ligament and peroneal muscles are considered to have a role in prevention of ankle sprains. It has been shown that after ten consecutive trials of ankle inversion (as if there is a lateral ankle spraining force), stretch reflex response amplitude decreased 20−50%, suggesting increased risk for injuries (Jackson et al., 2009).

Cognitive approaches

A major part of human learning consists of interplay between cognitive functions, such as thoughts, memories and expectations. Here, we consider observational learning and learning through imitation. The concept of *observational learning* was introduced by Albert Bandura. He demonstrated that children imitated the violent behaviors of adult models towards a toy (Bandura et al., 1963). This type of learning is very important for learning clinical procedural skills, such as injection, intubation etc. Imitation of a model is strengthened if the model is rewarded for that particular behavior. In humans,

observational learning is associated with mirror neurons, a group of neurons in the supplementary motor area and in the medial temporal lobe, which show response during both execution and observation of actions (Rizzolatti et al., 1996; Mukamel et al., 2010). Mirror neurons have been found to show response to specific type of goal-directed movements in upper extremity functions, such as grasping and facial emotional gestures. Therefore, it has been suggested that mirror neurons are important for interacting with objects, and also for social cognition particularly for understanding the actions of others (Heyes, 2010).

Memory

Memory is created through learning. It is defined as 'a theoretical term used to determine instances in which subjects' current behavior is determined by some aspects of his previous experience' (Domjan and Burkhard, 1982). Remembering threatening situations or locations where food has previously been found has an evolutionary importance. It is also meaningful for the energy system; if a motor behavior is repeated very often, it should be stored so when needed again, the neural and musculoskeletal systems consume less energy. Adaptation to repeated actions results in change in nervous and musculoskeletal systems. This ability to change is called plasticity. Neuroplasticity describes the change in synaptic properties of neurons in response to environmental stimulation, and in recovery from brain and spinal cord injuries (Merzenich, 2013). Neuroplasticity is greatest during childhood, when synaptic connections bloom and are pruned, but it has been known to persist through the life span, although to a lesser extent. A similar tendency of plasticity exists for skeletal muscles, which have great adaptive and regenerative capacity in response to environmental mechanical stimuli, exercise and injury throughout the life span, but particularly during early periods of development (Mersmann et al., 2014).

Memory may have several components, including visual, phonological or olfactorial. For example, memories of your mother may be triggered by hearing her name, smelling her perfume, seeing her photo, and hearing her voice. The memory can be divided into two categories; short-term and long-term memory (Fig. 25.2). Long-term memory may be further subdivided into different components in relation to how learning is acquired. This model is termed the multiple memory systems approach (Nyberg, 1996).

Short-term memory holds information for 15−25 s, and has a limited capacity (Feldman and Garrison, 1993). For example, you can hold a phone number in your short-term memory while dialing, but once dialed, it is forgotten. *Working memory* is a short-term memory buffer with a limited capacity. It describes the work-bench of the mind, where we hold the significant information active for ongoing mental process of comprehension, solving problems, and decision-making. Therefore, working memory is an important capacity during motor skill acquisition. Indeed, a stronger visuospatial working memory is associated with faster learning of manual skills in the early phase of practice (Anguera et al., 2010, 2011; Ruitenberg, De Dios et al., 2018). This association has been related to individual differences in explicit strategies used to achieve the manual task (Christou et al., 2016).

Long-term memory stores information on a relatively permanent basis, and is considered to have unlimited capacity within the inherent compounds of the brain. The declarative long-term memories can be consciously accessed and declared and has two distinct types; semantic memory and episodic memory (Fig. 25.2). An example for semantic memory is remembering the names of all objects associated with the color red. This gives us a semantic word tree, which is important in language learning. The second clearly defined type is episodic memory. This covers episodes, events in a person's life and conceptual issues such as subjective time and consciousness (Tulving, 2002). A type which cannot be declared is *procedural memory*, referring to *motor memory* for skills like cycling. This is a type of long-term memory; e.g. we never forget how to ride a bike, swim or play tennis.

Four different stages in memory formation can be defined: encoding and storing newly acquired information (encoding), transferring encoded information from an unstable state to a more stable state (consolidation), retrieving the information when needed (retrieval), and updating the information and re-storing it (reconsolidation). An important stage is consolidation, which stabilizes information in our memory. Motor memory significantly differs from declarative memory in consolidation phase. In every trial of the task motor memory has 'savings', a term used to describe a more rapid rate of relearning compared with the original learning (Krakauer and Shadmehr, 2006). If you have previously practiced a novel motor task, the next time you memorize the movement pattern, meaning that you relearn it faster because of 'saving' in the motor memory. Savings of motor learning have been observed after one day (Bédard and Sanes, 2011; Villalta et al., 2013; Seidler et al., 2016), one month (Della-Maggiore and McIntosh, 2005), five months (Shadmehr and Brashers-Krug, 1997), and even as much as one year after initial learning (Landi et al., 2011).

Savings can be better understood with online and offline processes during motor learning and formation of motor memory. Online process describes the gain or loss in motor performance during a practice session, and offline process refers to performance changes occuring between subsequent practice sessions (Dayan and Cohen, 2011).

Offline learning is related to neuroplasticity (Muellbacher et al., 2002), thereby the type of activity after the practice session might interact with the offline learning process. While sleep enhances offline learning (positive transfer) (Walker et al., 2003), performing interfering motor task has been shown to abolish motor memory consolidation (negative transfer) (Brashers-Krug et al., 1996).

Physiological approach

Motor learning or training induces structural and functional changes at neuronal level. These changes include increase in the number of neurons, reorganization or expansion of cortical motor and sensory maps, modulation of neuron's firing rate and synaptic transmission. These findings were shown in animal and human studies. Learning new acrobatic movements, rats showed increased number of synapses per Purkinje cell in cerebellum (Black et al., 1990). Also in motor cortex, rats trained on a skilled reaching task showed enlarged cortical representations of wrist and digit movements, and more synapses per neuron (Kleim et al., 2002). Functional reorganization of the human brain is shown in a study using TMS, which showed piano practicing expanded the cortical representation of finger movements (Pascual-Leone et al., 1995). Likewise, increased sensory-perceptual skills, for example auditory discrimination, is associated with the expansion primary sensory cortex (Recanzone et al., 1992; Recanzone et al., 1993), and sharpening neural tuning (Schoups et al., 2001). In another study about piano practice, increased white matter fiber tracts were shown (Bengtsson et al., 2005). The structure of white matter fiber tracts regulate the timing and speed of action potentials across axons. Neurons change their synaptic properties in response to transmission of action potentials. According to Hebb's learning rule, "neurons that fire together, wire together" (Hebb, 1949). Therefore, training-induced plasticity in the primary motor cortex may occur through lasting modulations in synaptic transmission, including synaptogenesis and the coordinated strengthening, e.g. long-term potentiation, and weakening, e.g. long-term depression, of synaptic connections.

Acquisition and retention of motor skill leads to structural and functional changes at cortical and subcortical levels in the central nervous system. These changes evolve over time and engage different brain regions. Functional magnetic resonance imaging (fMRI) studies suggested that prefrontal, parietal and partly hippocampal brain regions, in addition to sensorimotor cortical-striato-cerebellar networks, are active during the initial stage of motor learning (Kami et al., 1995; Honda et al., 1998; Floyer-Lea and Matthews, 2005; Albouy et al., 2008). The premotor area seems to play an important role to initiate new programs for movement and introduce changes in programs that are in progress. In later stages when the attention demand decreases, there is lower level of prefrontal activation (Poldrack et al., 2005).

The serial reaction time (SRT) task is a widely used motor paradigm used to study neural correlates of motor learning. In the SRT task, a stimulus appears on a computer screen, and the participant is instructed to press the specific key assigned to that stimulus as quick as possible. The order of stimuli follows a predictable order, but the participant does not initially know this. During the task, reaction time decreases as a result of motor learning. If the order of stimulus is changed, then the reaction time increases. In SRT, some individuals can verbally express the order of the stimulus, but even for those who cannot reaction time still decreases (Willingham et al., 2002). Neuroimaging studies make use of this paradigm to differentiate neural networks involved in implicit and explicit learning. The neural distinction between implicit and explicit learning comes from a case study, H.M. Surgical removal of bilateral medial temporal lobes resulted in loss of explicit, but not implicit learning (Corkin, 2002). In most cases of motor skill acquisition, both implicit and explicit components are present; an fMRI study neatly showed that basal ganglia is related to the implicit component of learning, and, the prefrontal cortex to the explicit component (Destrebecqz et al., 2005). These findings show the neural correlates of online motor learning. A newly acquired motor skill is transferred from an unstable to a more stable state during consolidation phase, or, in other words, during offline motor learning. Primary motor cortex (M1) has been found to be essential to early stage of motor consolidation. It has been shown that acceleration and muscle force generation of newly learned finger movements have been disrupted when M1 is stimulated by repetitive transcranial magnetic stimulation (rTMS) (Muellbacher et al., 2002).

Neural networks activated during motor learning are different from those activated during adaptation. During motor learning of, for example, typewriting, activation occurs in a large neural network of sensory and motor cortices in the frontal and parietal lobes, basal ganglia and cerebellum. In motor learning, initially whole network is active but later activity in cerebellum, but not the basal ganglia, decreases. In motor adaptation, however, the cortico-cerebellar network continues to be active, while the activity in the basal ganglia decreases (Forssberg, 2008). The role of cerebellum during motor adaptation is very prominent, since it was found to be important for predicting the state of the body during movement (Miall et al., 2007). The cerebellum estimates the sensory consequences of movement, and the response of the cerebellar neurons has been shown during motor learning of head movements. The difference between

motor command and motor output led to robust response of cerebellar neurons, demonstrating sensitivity of neurons to cerebellar predictions (Brooks et al., 2015). Further knowledge about the neural correlates of sensory motor adaptation is given in Chapter 27, The effects of weightlessness on human body: spatial orientation, sensory-integration and sensory-compensation.

Motor adaptation

Motor skill performance is dependent on the person, performance environment and the skill level interaction. Context differs every time we perform the task. Performance may be influenced by level of stress, emotional state, environmental factors, such as the ground, change in temperature, and even wind speed. Motor adaptation, usually termed sensorimotor adaptation, is the ability to adjust behavior to changing environmental or internal demands to execute appropriate, goal-directed motor performance. Briefly, the difference between motor learning and motor adaptation is that in the former a new motor program is learned and, in the latter, a pre-existing motor program is adapted. Because of adaptation, movement may change in pattern of force or direction. It requires the modification of the movement based on error signal (Martin et al., 1996). The error signal is the difference between the brain's predicted outcome of the movement and the observed movement; the nervous system needs to reorganize itself to reduce this signal (Tseng et al., 2007). Once adapted to the new condition, individuals cannot easily readapt their prior behavior; instead, they must 'de-adapt' it with practice (Bastian, 2008).

A good example for adaptation and de-adaptation is a 'backwards' bicycle (Sandlin, 2015), i.e. one in which turning the handlebar to the left makes the wheel go to the right, and vice versa. So, riding the backwards bike require adaptation of balance and postural control in a totally opposite way to normal. In the video of this experiment, riders struggle with their balance and fail to progress even a few meters. The inventor of the backwards bike, Mr. Sandlin, reported that he learned to ride it in eight months, while his six year-old son took only two weeks. Both father and son were used to ride 'normal' bikes, but the son adapted to utilizing 'backwards' bike much faster because of higher level of neuroplasticity during childhood. Once adapted to the backwards bike, Mr. Sandlin reported that he had difficulty of de-adaptation to normal bike again and needed to practice (Sandlin, 2015). Sensorimotor adaptation and de-adaptation processes are probably more experimented in astronauts. Astronauts are unique group, exposed to microgravity and disrupted sensory information during their mission in space. The nervous system must organize sensorimotor information in space and reorganize it upon arrival to Earth. Astronauts face deficits of perceptual and motor functions on return to Earth. The average de-adaptation time for functional mobility of astronauts following six-month stay in space was found to be 15 days (Mulavara et al., 2010). Recent research in this field attempted to enhance sensorimotor adaptability through training that is dependent on practicing sensory variations of the task (Bloomberg et al., 2015). In this practice, astronauts use a special treadmill, whose walking surface can be manipulated to provide challenges to gait stability. Also, discordant visual stimuli is provided by a virtual visual scene, ensuring that gait and posture need to be adjusted to several sensory variations (Bloomberg et al., 2015). In this and similar attempts, the ultimate aim is learning to learn, in other words, to train nervous system to adapt to changing situations faster and more efficiently.

Stages of motor learning

All of those who are introduced a novel skill are very naive at the beginning, but improve their performance with practice. In the skill acquisition process, we observe differences of the following performance characteristics: improvement, consistency, stability, persistence, adaptability, and reduction of attention demand (Magill and Anderson, 2007). First of all, over period of time, performance improves. Second, as learning progresses, we see a more consistent and stable performance from one trial to another. Persistency describes the capability of showing improved performance over increasing periods of time; e.g. days, weeks or months. Adaptability or generalizability is an important aspect of performance related to skill learning. It refers to adaptation to changes in personal, task, and/or environmental characteristics. Lastly, motor learning leads to reduction in attention demand, allowing an individual to show dual-task performance, such as conversing while juggling balls.

Most of the motor tasks require optimization of both speed and accuracy. For experts such as professional athletes, the goal is to perform a task as quickly and accurately as possible. According to the well-known Fitts' law, movement time (speed) can be predicted when the distance to the target, and the width of the target are known (Fitts, 1954). The formula of Fitts' law is $MT = a + b*\log_2 (2D/W)$. Movement time (MT) scales as a logarithmic function of the ratio of movement distance (D) to the target width (W), where *a* and *b* are coefficients.

Derived from the Fitts' law, there is speed-accuracy trade-off, which defines the decrease in the movement speed when the task requires more accuracy; for example, to thread a needle, a certain degree of slowness is needed to push the thread through the eye. If you speed the movement up, the thread would target a larger target area, as

can be derived from the formula. The question is whether Fitts' law holds its predictive value during motor learning, since during learning, movements become faster and more accurate while target distance and target width remain the same. The answer is that Fitts' law is still found to be valid, but with changed coefficients (Latash, 2012).

The distinct stages of motor learning have been defined by certain models. Despite different terminology and stages defined, all models essentially agree on the main characteristics of the learning process. Below, the models are briefly described.

Fitts and Posner three-stage model proposes a process of cognitive, associative and autonomous stages. This model highlights that in the early stages of learning there is much higher cognitive demand, such as problem solving, working memory and attention until the skill becomes automatic (Magill and Anderson, 2007).

Bernstein's three-stage model focuses on the changes in motor control in consecutive stages of motor learning. In order to understand his theory, it is important to understand the degrees of freedom problem. The number of independent components and how each component can vary creates numerous degrees of freedom for the motor system. For example, in order to reach object, many muscles and joints have to be controlled by the nervous system. During motor learning, Bernstein suggested that the motor system has to solve this problem. At the first stage, he proposed an inhibitory pattern that there is an elimination of, or *freezing, redundant degrees-of-freedom* to simplify the control of the movement. In the second stage, control becomes more comfortable, which is associated with *releasing degrees of freedom* that were previously frozen. In the last stage, there is an *optimal interaction with external forces* that leads refinement of control strategies, meaning that a person learns to use, rather than fight against external forces (Latash and Turvey, 1996). Bernstein's model was experimentally supported; a recent finding in transtibial amputees confirmed the freezing and releasing stages during lower limb joint flexion and extension (Wurdeman et al., 2014).

There is also a two-stage model proposed by Latash, which relies on the changes of motor synergies. According to this model, variance of performance characteristics can be viewed as having two components; *good* and *bad variance* . In the first stage, bad variance decreases while good variance shows almost no change, which strengths the motor synergy. In the second stage, bad variance decreases as much as possible, while good variance decreases to the optimum level, which weakens the motor synergy. With practice, bad variance decreases so, for example, accuracy of performance increases (Latash, 2012).

Ann Gentile proposed another two-stage model with a perspective on the learner's goal. In the *initial stage of learning* , movement pattern is acquired and the conditions in the environmental context are learned and identified in order to achieve the action goal. In *later stages*, she highlighted improvement in three characteristics of the action: adaptation, consistency and economy of effort. She also proposed that learner's goals depend on the type of skill practiced (Gentile, 1972). In *closed skills*, learner shows fixation on the movement pattern learned in the initial stage, and refines it to achieve consistency and economy. An example of a closed skill is writing with the same type of pen on the same type of surface. *Open skills* require the learner show diversification of the basic movement pattern learned in the initial stage, thereby motor adaptation. Gentile's perspective provided a framework for goal-directed training for rehabilitation settings (Mastos et al., 2007).

The final model is Halsband's three-stage model, defined in neuropsychological terms as follows: In the *initial stage*, performance is under close sensory guidance, and the accuracy and speed of performance varies greatly from trial to trial. In the *intermediate stage*, sensory-motor connections become stronger; movements become faster, and more accurate, and are executed with smaller variance. In the *advanced stage*, performance is fast, automated, and skillful, with isochronous movements and whole sensory field control (Halsband and Freund, 1993). Halsband's model was demonstrated in a study where individuals were trained with auditory information for reach-and-grasp task. This task was designed to give auditory information regarding the size of the objects to grasp to allow individuals to establish a new audiomotor map. They found no overt signs of learning in the first approximately 10−15 trials; subjects used the maximum grip aperture to achieve the task. This was followed by a period of fast learning, where individuals adjusted the hand grip according to the size of the object via auditory information, and in the final stage they reached a plateau of learning (Säfström and Edin, 2006).

Learning skill in different life stages

Not all behavioral changes result from learning. Phylogenetic memory was shaped during evolution, and results in some innate behavioral responses, such as fear. Recent study in mice showed the strong memory traces of fearful experiences in subsequent generations. Fear response to conditioned odor was found to enhance neuroanatomical representation of the odor in the brain and, more importantly, this was selectively transmitted to next generations (Dias and Ressler, 2014). What about human behaviors? How much genetics and experience contribute to learning? This question touches the controversy of the

effect of 'nature versus nurture' on development. Developmental studies, especially on infants, have investigated whether genes predetermine motor development, or whether it is a result of practice and interaction with the environment.

According to the developmentalist Gesell (1934) motor development or acquisition of motor skills such as rolling, sitting, standing, walking appear in a sequence and within specific periods during infancy, emphasizing the role of genes in unfolding development of motor skills (Gesell et al., 1934). On the other hand, recent dynamic systems theory suggests that motor development is not a simply passive process in which genes dictate the developmental milestones over time. Rather, infants actively perceives and acts upon the constraints set by their bodies and environment to achieve a goal. Therefore, according to other developmentalists, infants assemble motor skills for perceiving and acting (Keen et al., 2014). However, experiments such as the "visual cliff", suggest that infants are born with depth perception that directs their motor skill acquisition (Feldman and Garrison, 1993).

Myelination is very important for motor skill development during childhood. Training or practice during childhood has very prominent effects on myelination. Motor practice induces the neural activity in fiber tracts, and therefore induces myelination. In a study by Bengtsson et al., in which they compared the neural correlates of extensive piano practicing during childhood, adolescence and adulthood, they found regional specific changes in pyramidal tract. Most importantly, largest number of brain regions correlated with childhood practicing, even compared to much more intensive practice in adulthood. This example explains the interaction between nature and nurture, and indicates a developmental window in which white matter plasticity is highly favored (Bengtsson et al., 2005).

Older adults is another group for whom it is important to consider for motor learning. Increase in aging population and longer life expectancy in many countries highlight the motor learning capacity and plasticity in this group. With increasing age, musculoskeletal and nervous systems, and sensory organs are negatively affected. Seeing, hearing, touching are important sensory functions for motor system, and decline in these sensory functions are significant in individuals 75 years and older (Santrock, 2006). According to a study, older adults take longer to move than young adults, and this difference remains for both easy and difficult movement tasks (Ketcham and Stelmach, 2001). With these information, it is no surprise that perceptual-motor coupling is declining, and leading problems for already learned motor skills such as driving (Santrock, 2006). On the other hand, learning new motor skills is intact, but with a slower rate. In a study, six days of training in a novel task, juggling,

with participants aged in 6 to 89 years showed the performance of older adults was comparable with those of children and young adults. The study showed the best outcome for teenagers and young adults between 15 and 29 years (Voelcker-Rehage and Willimczik, 2006).

Motor learning in expertise

Experts are a special group of people who develop skillful actions above the level of normal performance. The area of expertise can be in cognitive domains like science, mathematics, chess-playing, or in motor domains such as athletics, piano playing or ballet. There are some key characteristics of experts. First, they deliberately practice the skill for extensive periods. Second, they have a strong interest in the skill, and thereby, motivation. Lastly, they prioritize skill training over other significant daily life activities. In motor learning, experts are a valuable group for investigating enhancement of performance of a learned or highly experienced motor skill.

Musical expertise in piano players has been extensively studied by Fredrik Ullen's research group. They measured the amount of practice (total hours of practice) during different developmental periods; childhood, adolescence and adulthood, both in piano players and in nonmusicians. Longer practice time and white matter changes were found in all groups, regardless of age. Age was generally found as a strong predictor for brain development. However, this finding may show that practice may hinder the age-development relationship (Bengtsson et al., 2005). Macro anatomical changes have been observed in musicians. Increase in cortical gray matter volume and higher fractional anisotropy in white matter have been reported. These changes have been shown in the corpus callosum, motor cortex, cerebellum and planum temporale of musicians (Schlaug, 2015). Cortical excitability has also been shown after long-term motor training; musicians showed less interhemispheric inhibition (Nordstrom and Butler, 2002).

Expertise in professional athletes has been one of the most intriguing areas in the field of motor learning. Recent technological advances in methods to study kinesiology provided valuable data. Video-based analysis of technical movements showed that famous football player Lionel Messi makes more use of dribbling and feint of change of direction than Cristiano Ronaldo, meaning that Messi showed variability, and was more unpredictable (Castañer et al., 2017). It has been shown that humans predict others' actions by using bell-shaped velocity profile (Stadler et al., 2012). However, data that movement of Messi is unpredictable, i.e. he does not fit into this bell-shaped velocity profile. A study by Anderson and Sidaway showed that as an acute result of practice, novice soccer players increased linear velocity

of the foot in relation to changing pattern of coordination underlying the movement (Anderson and Sidaway, 1994). Trial-to-trial variability in the execution of movements is usually considered a drawback of the noisy sensory motor system, however, recent studies have suggested that motor variability may also be a feature of how sensorimotor systems operate and learn. This view stems from the reinforcement learning theory, and sees motor variability as purposeful exploration of motor space that can drive motor learning (Dhawale et al., 2017).

The variable practice, rather than repeating the same task, is favored in athlete training programs (Li and Lima, 2002; Shoenfelt et al., 2002) because sensorimotor adaptation leads to a high level of plasticity and learning effect, which in effect teaches the system to learn to learn. Schmidt's schema theory of motor learning suggests that the motor system creates a library of motor actions (schemas) for classes of motor problems (Schmidt, 1975). In each trial, the performer stores the initial condition, specific surrounding, sensory consequences and the outcome of the movement. Over trials, varying conditions of practice allows the motor schema to become optimized. When a novel motor task is presented, the person, if trained with variable practice, is able to retrieve the appropriate movement patterns more efficiently (McCracken and Stelmach, 1977; Shea and Morgan, 1979; Catalano and Kleiner, 1984; Sherwood, 1996).

Another focus in athlete training has been on whether implicit or explicit processes lead superior performance, and accordingly, which components of performance benefits. It has been found that implicitly learned motor skills tend to be stable under performance pressure (Hardy et al., 1996; Mullen et al., 2007) and physiological fatigue (Poolton et al., 2007; Masters et al., 2008), and also demand less attention (Maxwell et al., 2003; Poolton et al., 2006). Due to difficulties in designing experiments involving implicit and explicit learning, there are only small number of studies. In one study (Lam et al., 2009), in modified basketball shooting task, three groups were compared after receiving three-day training. The first group received explicit learning via eight technical instructions, the second group received implicit learning via single analogical instruction, and the final group received no instructions. No performance differences were found between groups in retention tests, indicating that there was no difference between learning models. However, in transfer test, despite the lack of any kinematic changes, performance deteriorated for both explicit and control groups, but not for the implicit group.

Disability of motor learning

Disability of motor learning can be seen in diseases that affect nervous and musculoskeletal systems, and sensory organs. More intriguingly, it can be seen during childhood development without any apparent physical or intellectual problem. Developmental Coordination Disorder (DCD) is one of these developmental disorders. In DCD, children fail to learn complex coordinated movement skills, such as riding a bike, or handwriting. Motor learning problems recently proposed as an explanation of co-occurence of neurodevelopmental disorders such as ADHD, dyslexia, language impairment and DCD. The "procedural deficit hypothesis" suggests that commonly observed clumsiness and learning deficits in these mildly effected groups are results of procedural (or motor) learning deficit (Nicolson and Fawcett, 2007). We use the motor learning system to acquire the movement patterns to produce speech sounds and motor actions. During development, most affected by motor learning deficit are speed and accuracy of manual movements during complex task, e.g. drawing or handwriting, and articulation of complex speech sounds. Attention mechanisms are known to be important in the initial phase of motor learning. Consequently, impairments in speech and motor domains, which require learning of complex sequence of movements, are commonly observed in neurodevelopmental disorders. Childhood Apraxia of Speech is considered as a neurodevelopmental disorder that exhibits the deficit in motor learning, because affected children showed lower performance both in speech and complex manual skills such as drawing (Tükel et al., 2015). Autism Spectrum Disorders (ASD) is another group with defined motor learning difficulties, despite the absence of any brain lesion or malformation (Ming et al., 2007).

Motor learning in rehabilitation

The primary goal of rehabilitation is to induce neuroplasticity from cortex to spinal cord for restoring motor and cognitive skills. Motor learning principles are used in the rehabilitation context to facilitate neuroplasticity and motor recovery. Experiments in healthy subjects highlighted that practicing the task under varied sensory stimuli, rather than repeating the same task in stable conditions, leads to better outcomes that can be described as faster adaptation (Roller et al., 2001). This means that the sensorimotor system learns to adapt to changing conditions better, in other words, the system is more plastic. This principle has been transferred to therapeutic approaches in Down syndrome (Latash et al., 2002), and to neurorehabilitation of stroke patients (Krakauer, 2006).

Rehabilitation programs in stroke patients showed the potential variation in groups with different severity of dysfunctions. In a study by Hardwick et al. 4-day training was given to stroke patients and healthy controls. Stroke survivors were divided into two groups according to

motor impairment: mild-to-moderate and moderate-to-severe. Groups practiced isometric contractions of elbow flexors to navigate an on-screen cursor to different targets for 4 days. The speed-accuracy trade-off function was assessed for each group before and after the training, and controlled for differences between individuals in self-selected movement speeds. All groups were able to improve their performance through skill acquisition. The moderate-to-severe group reached the baseline performance of the mild-to-moderate group, and the mild-to-moderate group reached the baseline performance of the control group (Hardwick et al., 2017). Robot-assisted therapy seems to have strong potential for improving upper limb function in stroke patients. It was shown more effective than usual care when applied for 12 weeks and 36 weeks; however, intensive therapy outperformed robot-assisted therapy (Lo et al., 2010).

There is a greater amount of research on motor learning during development in the case of brain lesion in children with cerebral palsy (CP) conducted by Ann-Christin Eliasson's research group. Sensorimotor reorganization of the central nervous system, in case of early brain lesion, shows an impressive capacity for compensation and preservation of functional motor skills. In unilateral CP, contralateral corticomotor projection pattern was found important for the speed and accuracy of reaching, grasping, releasing and functional tasks (Holmström et al., 2010). Two weeks of motor training with constraint induced movement therapy (CIMT) improved manual skills irrespective of corticomotor projection pattern and brain lesion characteristics (Islam et al., 2014). Motor learning of handwriting skill has also been investigated in children with unilateral CP, and findings indicated a slower rate of learning in motor skill acquisition, which can be predetermined by chronological age and IQ score (Fig. 25.3) (Tükel Kavak and Eliasson, 2011).

Observational learning and the so-called 'mirror neuron system' has become one of the most promising approaches in rehabilitation. During the last decade, various studies were carried out regarding the clinical use of action observation for motor rehabilitation of sub-acute and chronic stroke patients. Mirror neurons are a specific class of neurons that are activated and discharge both during observation of another individual's motor act, and during the execution of the same or similar motor act (Rizzolatti et al., 1996). By using TMS and fMRI, different studies have demonstrated the presence of the mirror neuron system and their mechanism in humans. Studies have demonstrated the activation of brain areas involving inferior parietal lobe and the ventral premotor cortex, as well as the caudal part of the inferior frontal gyrus, when individuals learn motor actions via execution, imitation, observation and motor imagery. This means that observing or imagining an action can affect cortical excitability

FIGURE 25.3 A child with unilateral cerebral palsy (CP) is shown during handwriting test. Learning handwriting refers to copying readable letters therefore; it requires speed and accuracy of fine motor movements along with visual perception and visual working memory. Children with unilateral CP usually use their non-effected hand for handwriting while using their effected hand to stabilize the paper as shown in the picture. Motor learning of copying readable letters take longer time period for children with CP compared to those of their typically developing peers. Learning rate in CP group can be predicted by age and IQ.

and facilitate subsequent movement execution. The intention to imitate movements shown on a video resulted better outcome for functional upper limb dexterity for stroke patients (Franceschini et al., 2012). Similarly, for Parkinson's disease, imitation of motor actions seems a promising rehabilitation tool (Caligiore et al., 2017). In healthy individuals, observational motor learning has been found very effective for implicit learning of sequential complex motor skills. Findings from SRT task showed that subjects can acquire sequence information by watching another person performing the task, and observation results in as much sequence learning as task practice. This study also showed that sequence knowledge acquired by model observation can be encoded motorically (Heyes and Foster, 2002).

Since 1994; when Salinas & Abbot showed that the direction of resulting limb movement can be computed from measurements in fewer than 100 primary motor cortex cells (Salinas and Abbott, 1994), the activation of primary motor cortex has been used to guide prosthetic limb in prosthetic rehabilitation, suggesting applications for patients with amputated or paralyzed limbs. One study demonstrated that two tetraplegic patients could exert some control over the speed and direction of movement of a computer cursor based on recording of 96 neurons in the dominant hand area of the primary motor cortex (Kim et al., 2008). In a more recent study, Hochberg et al. showed that tetraplegic patients are able to move a robotic arm for reaching and grasping, and in one case, use the robotic arm to drink from a bottle (Hochberg et al., 2012). Of course, there are high levels of variation between

individuals in these experiments. The impressive finding is that individuals show neuroplasticity and can learn to fire their motor neurons to control the robotic arm.

In rehabilitation setting, studies also highlight the strong relationship between motor learning and emotional and motivational factors, thus are often use the words 'goal-directed' or 'targeted' to describe a movement, because all movement has an aim. Motion, cognition and emotion are interconnected, faster and more efficient motor learning can be facilitated by motivation and cognition. This interaction is well-known by clinicians working with patients during the recovery phase, but without tools to motivate the patients, is often overlooked. It is important to emphasize that rehabilitation settings require either interdisciplinary teamwork, or interdisciplinary-equipped clinicians who can develop therapeutic approaches that fuel motion-cognition-emotion interaction.

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