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Locomotor adaptation: Significance and underlying neural mechanisms

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Abstract Human locomotion is flexible in meeting the requirements of given environmental or task demands. Hence, in everyday life, we can walk, run, and skip in environmental surroundings that vary from hour to hour and even from second to second. In making such flexible adjustments, a sense of “adaptability” attained by the central nervous system plays an important role. In the literature, adaptation studies focusing on locomotion have attracted a great deal of attention in recent years for their potential application to the designing of gait training programs, and as a useful method for revealing the specific mechanisms underlying human locomotion. In this review article, to address how locomotor adaptation is related to social locomotion, the authors introduce knowledge accumulated in recent decades, particularly that related to two different types of locomotor adaptation studies: first, studies that address the general features of locomotor adaptation including underlying neural mechanisms, and second, those that use experimental paradigms of locomotor adaptation to reveal the context-dependency of locomotion. It should be noted that, although knowledge of locomotor adaptation has been increasing, the field is still largely unexplored, and further intensive research in the future is necessary.

Keywords: locomotion, walking, running, adaptation, specificity

Introduction

In everyday life, humans use locomotion (walking, running, skipping, and so on) to move through space. It has been well documented that locomotion is not simply an accumulation of either voluntary- or reflex-induced movements. Instead, a specialized functional network in the spinal cord (known as central pattern generators, or CPGs) (for review, see Ref. 1) is known to exist and play a significant role in the generation of patterned motor outputs. The patterned motor outputs, in turn, result in movement of the limbs. Because of characteristic features of the functional network, locomotive movements are often regarded as stereotypical. An example illustrating such stereotype can be found in a unique behavior of human infants. In an upright standing posture with external support, they exhibit patterned stepping-like lower-limb movements upon their center of mass moved forward; this is indirect evidence demonstrating the existence of CPGs. Similar aspects have been demonstrated in cats that have undergone spinalization⁵, that is, cats without any descending input from the higher centers. Despite the stereotypical movements present in the basic aspects of locomotion, when utilizing locomotion in our daily lives we always have to adjust to changing environmental and task demands. For example, road surfaces are not always flat and smooth; there are variable constraints such as unevenness, gradient, slipperiness, and many others. We often wear different types of apparel and shoes, and carry items with different weights and shapes from day to day. Regarding the task demands, we not only walk, but also run and skip and perform any number of other locomotive tasks, and we do so at a variety of speeds. Regardless of the changing environmental surroundings and task demands, however, we as adult humans can achieve constant locomotion in any number of situations. Locomotion, therefore, not only a stereotypical behavior, but is also flexible enough to accommodate widely varying situations. In this review article, the authors present an overview of the neural mechanisms through which humans exercise flexible control of locomotion.

Significance of adaptation in social locomotion

The fact that we can execute smooth and skilled movements in a variety of situations is largely dependent on
our past experience. That is, the generation of motor patterns to attain such movements occurs through repetitive practices on the basis of “trial and error” processes. In other words, any movements without a past precedent (for example, upon the first exposure to particular environmental surroundings or motor tasks) cannot be executed smoothly. An example of this “trial and error”-based accumulation of skilled movement is given in the following story reflecting an everyday situation.

A boy began his locomotion by crawling at eight months, and he started walking at around 12 months old. Now, at two years of age, he has more than 12 months of walking experience and shows smooth and skillful walking movement. He can walk even under varied physical constraints such as uneven road surfaces, slopes, stairs, and other constraints in his everyday surroundings. One day, he went shopping with his parents at a nearby supermarket, and was attracted to an escalator that he saw for the first time in his life. As he saw people stepping onto the “moving stairs”, he also wanted to get on; and so he walked over to the escalator and stepped on it. Upon contacting the surface of the moving escalator, his leg was pulled forward, his center of body mass moved backward, and he fell.

As stated above, he had enough experience to walk normally. That is, he already had the motor strategies in the central nervous system (CNS) that made him capable of walking in a variety of possible contexts in everyday life. Lack of a motor strategy for a context to which he was newly exposed (stepping onto the moving platform of the escalator, therefore, a trial) could have been responsible for the fall (error). In later attempts to step onto an escalator, he would perform better; and through practice (further trials), he would acquire more sophisticated motor strategies and better ways to step on it (thereby minimizing the error). This acquisition of motor strategies by the CNS is referred to as “motor adaptation” or “motor learning”. Below, an overview of the mechanisms underlying motor adaptation is provided on the basis of studies executed mostly in the last decade.

**Experimental findings related to locomotor adaptation**

This review deals with locomotor adaptation, a notion that may appear strange to many readers. This is because locomotion such as walking and running are motor tasks that are frequently practiced in a variety of different contexts in everyday life beginning in childhood (unlike those requiring practice such as juggling and playing musical instruments). To study locomotor adaptation and therefore to enhance adaptation in adult humans, exposure to a novel environment that is not available in everyday life is necessary. Furthermore, to quantitatively analyze the adaptive phenomena, the subject has to be exposed to the novel environment both systematically and with reproducibility. In recent studies focusing on locomotor adaptation, it was typical to use an experimental apparatus such as the following: 1) Robotically-controlled gait orthosis either to enhance or to interfere with joint movements at particular phases of locomotion, 2) Specialized treadmill (split-belt treadmill) with two belts (one underneath each foot) operated at independent velocities, and 3) Application of a force field during the swing phase of locomotion through the use of a weight load or elastic rubber band. In any of these cases, the subjects’ normal gait patterns are transiently interfered with through the imposition of novel physical constraints. In the minutes after this imposition, they acquire motor patterns that are appropriate under the respective constraints.

**Basic knowledge of locomotor adaptation**

Studies focusing on motor adaptation, as opposed to locomotor adaptation, have been well established in simple motor tasks and particularly among simple reaching movements of the upper extremity. When a person reaches a hand toward a target in front of him or her, the hand generally creates a nearly straight trajectory toward the target. With the repetition of such a movement, a sudden and unknown imposition of force fields results in a deviation of the trajectory toward the direction of the force field. Through repetitive practice of the movement in the force field, however, the nearly-straight trajectories are restored. At this point, a sudden and unknown removal of the force field causes the deviation of the trajectory, this time in the direction opposite to the previously imposed force field. The neural mechanisms underlying these phenomena are described below.

In the CNS, a dynamic model of the musculoskeletal system (known as the “internal model”) is developed on the basis of past experience. We can, therefore, easily reach our hand to a given target under normal conditions without constraints. The deviation of the trajectory (the difference between the target trajectory and the actual trajectory) upon exposure to the force field is detected as an error. Based on the error, the CNS updates the internal model (that is, it recalibrates the motor output) to minimize the error on a trial-to-trial basis. The subsequent deviation of the trajectory in the direction opposite to the force field is therefore regarded as occurring due to the emergence of motor output necessary to achieve the desired trajectory under the force field.

In the adjustment of motor output seen in these phenomena, the CNS is engaged in two different ways depending on the speed of the movement, namely feedback and feedforward control. In slow movements, the CNS continuously monitors the movement error and makes online (or real-time) corrections of the motor output (feedback control). Adjustment of the motor output through the feedback control involves a time delay due to limitations in the conduction speeds of the nerves and of transmission between them, and is therefore inappropriate for con-
trolling fast movements. Feedforward control is therefore necessary. In feedforward control, the CNS refers to the movement error in the previous trials (the feedback error) and predictively adjusts the motor output that is necessary to achieve the desired movement trajectory in forthcoming trials. The relative contributions of feedback and feedforward control can be modified by variable factors such as the movement speed and the subjects’ proficiency in the motor task. Regarding locomotor adaptation, it is possible that the neural mechanisms, as in the above-mentioned arm reaching movement, are shared partially or at a certain level. For the most part, however, the mechanism remains unclear since the notion of locomotor adaptation was only recently recognized and requires further elucidation. Here we provide a description of what is known about locomotor adaptation at present.

Reisman and colleagues developed an experimental paradigm utilizing a split-belt treadmill, and revealed the general features of locomotor adaptation from the perspective of both the temporal and spatial aspects of human walking. Lam et al. and Blanchette and Bouyer, by applying a force field during particular phases of walking, revealed phase-specific contributions of both feedback and feedforward control. With regard to the emergence of adaptive phenomena in locomotion, several studies have suggested possible neural mechanisms. For example, it was demonstrated that adaptation takes place in human infants. This potentially agrees with the findings of Hodgson and colleagues who demonstrated a similar adaptive nature in spinalized cats. These studies therefore showed that locomotor adaptation may occur as a reflection of the neural mechanisms inherent in the spinal cord. On the other hand, other studies showed that the cerebellum plays a significant role in locomotor adaptation. In patients with cerebellar lesions and cats that underwent experimental deprivation of cerebellar-induced long-term depression (LTD), an aspect of locomotor adaptation that is present in healthy individuals was impaired. These results, despite the difference in their viewpoints, suggest the possibility that locomotor adaptation can occur as long as a particular site in the CNS is intact.

**Context-dependency of locomotion revealed by locomotor adaptation paradigms**

The study of locomotor adaptation not only provides us with knowledge useful in the construction (or reconstruction) of locomotion after particular CNS lesions, but also has revealed the context-dependency of locomotion, which implies the existence of independent neural mechanisms that are capable of managing different tasks and environmental constraints. This context-dependency is the reason that, as we stated earlier, movements without past experience (for example, first exposure to particular environmental surroundings or motor tasks) cannot be executed smoothly. We therefore have to train in the respective contexts and acquire motor programs capable of movements under each context. Here we describe some examples of the context-dependency underlying particular locomotion movements.

The first example of context-dependency in locomotion was provided by Choi and colleagues in 2007 by utilizing a locomotor adaptation task on a split-belt treadmill. They revealed the existence of independent neural mechanisms for walking forward and backward. They also demonstrated that adaptation is dependent on the limb (left or right). Even when walking in the same direction (forward), it was subsequently demonstrated that there were independent neural mechanisms that corresponded to different walking speeds. Locomotor adaptations that took place at particular walking speeds were valid only at those specific speeds and did not transfer to others. Further, the authors demonstrated that even for locomotion at a single speed, the neural mechanisms underlying walking and running independently represented different modes of locomotion. In the experiment, after subjects adapted to walking on a split-belt treadmill (with a 2:1 ratio between speeds) for 10 minutes, the movement patterns when subsequently walking under a normal belt condition (two belts at the same speed) showed prominent asymmetry. Adapting to running on the split-belt treadmill also resulted in asymmetric movement when running afterward under a normal belt condition. However, the acquired (asymmetric) movement patterns in the respective gaits (walking or running) were not shared between the two gaits. That is, the subjects could walk normally (nearly symmetrically) after adapting to running asymmetrically, and could also run normally after adapting to walking asymmetrically. In the same study, further analyses showed interesting results. As stated above, although the subjects could walk normally after adapting to running asymmetrically, their movement resulted in prominent asymmetry when they started to walk subsequently (after running normally). A similar tendency was detected after adapting to walking asymmetrically. The acquired movement patterns in the respective gaits were therefore maintained independently of each other. In the results, since the use of joints and muscles may be largely shared between the two gaits, the limited share of the acquired movement patterns was surprising. Although the specific mechanisms cannot be directly addressed in a behavioral study, possible candidates will be considered based on the results obtained in animal studies. In the supraspinal mechanism, for example, the mesencephalic locomotor region (MLR) plays a significant role in determining different gaits. Electrical stimulation of a particular site in the MLR determined the initiation of different gait modes in decerebrated cats and different swimming behaviors in salamanders that were both dependent on stimulus intensity. Regarding the spinal cord, McLean and colleagues demonstrated in larval zebrafish that particular sets of swimming-related spinal interneurons were re-
cruted depending on the swimming frequency. A group of interneurons that was active under one movement frequency was strongly inhibited under others. More recently, in mice, experimental lesions in particular subtypes of locomotion-related spinal interneurons resulted in the impairment of normal alternate (left-right) locomotion, and the impairment occurred depending on stepping frequency. Other results have shown mode-dependency in the propriospinal neurons during scratching movement of a turtle hind limb.

In locomotor adaptation studies attempting to elucidate the context-dependency of the underlying neural mechanisms, the interpretation of the results is somewhat speculative, and the detailed mechanisms therefore remain unclear. These studies are, however, very important from the perspective of designing training regimens in that there was certain specificity at the behavioral level, i.e., the final output of the motor systems. Moreover, these behavioral results provide further motivation for revealing the more specific mechanisms underlying them.

Summary

In spite of the stereotypic quality of the basic mechanism of human locomotion, locomotion is also flexible enough to accommodate a variety of environmental and task demands. The notion of locomotor adaptation has been recognized only recently in the scientific literature, and more studies are necessary to elucidate further details. However, the adaptation concept is closely linked to what we experience in our everyday life, and any practice of locomotive movements can be regarded as an example of locomotor adaptation. Further studies on locomotor adaptation therefore can function to provide an objective, scientific understanding of our experience and may lead to the establishment of locomotion training protocols in a variety of situations such as sports training and those after particular CNS lesions.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this article.

References

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