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Locomotor body scheme

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ABSTRACT

The concept of body schema has been introduced and widely discussed in the literature to explain various clinical observations and distortions in the body and space representation. Here we address the role of body schema related information in multi-joint limb motion. The processing of proprioceptive information may differ significantly in static and dynamic conditions since in the latter case the control system may employ specific dynamic rules and constraints. Accordingly, the perception of movement, e.g., estimation of step length and walking distance, may rely on a priori knowledge about intrinsic dynamics of limb segment motion and inherent relationships between gait parameters and body proportions. The findings are discussed in the general framework of space and body movement representation and suggest the existence of a dynamic locomotor body schema used for controlling step length and path estimation.

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1. Introduction

Path integration

Locomotion

In order to perceive and act, the nervous system must be able to relate the positions of the body parts to one another and to a representation of the external world. This is achieved by an internal model of the configuration of the body and its orientation in space – the body schema. Head and Holmes (1911–1912) distinguished two principal aspects of the body schema: the position and

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movement of the body and the location of tactile stimuli on the surface of the body. Many separate classifications of "body schema" and "body image" have followed this original definition (see for review Cardinali, Brozzoli, & Farnè, 2009; Tiemersma, 1989). Proprioception plays a crucial role in position sense and also in conveying information about the positions of body parts relative to one another (Goodwin, McCloskey, & Matthews, 1972; Massion, 1992) and thus its loss drastically impairs the body schema (Blouin et al., 1993; Lajoie et al., 1996). The body schema has both adaptable (when using tools or when a child grows, etc.) and conservative (e.g., permanent phantom limb sensations in persons who got amputated) features. How the body schema is generated centrally is largely unknown, but it definitely encompasses various levels of the central nervous system (CNS). Different aspects of body schema may be processed by different neural networks.

There are a number of indications that it must exist at higher CNS levels, but there are other indications that a reduced form of body schema may also exist in the spinal cord (Poppele & Bosco, 2003; Windhorst, 1996). For example, populations of spinocerebellar neurons encode global parameters of the limb kinematics, i.e., limb length and orientation, rather than specific local information about muscles or joints that might be expected from their sensory input (Bosco, Poppele, & Eian, 2000). It has been shown that the isolated spinal cord of frogs incorporates a body schema. During the wiping reflex carried out by the hindlimb in response to some noxious skin stimulus on the forelimb, the precise movement trajectory depends on the position of the forelimb, indicating that the spinal cord has some internal representation of the forelimb's position (Fukson, Berkinblit, & Feldman, 1980; Giszter, McIntyre, & Bizzi, 1989). Recent studies on animals suggest that in the absence of any input from supraspinal structures, the lumbar spinal cord is capable of correcting kinematic errors in hindlimb coordination through practice (Heng & de Leon, 2007).

The notion of body schema (sometimes under the rubric of internal model or internal representation) has received attention in a large context of contemporary motor control (see for review Windhorst (2007)). For instance, the planning and learning of movement require an internal model of the limb's dynamic properties (Krakauer, Ghilardi, & Ghez, 1999; Shadmehr & Mussa-Ivaldi, 1994) and various computational approaches have been proposed to describe empirical data generated by observation and experiment for understanding a range of processes such as state estimation, prediction, context estimation, control, and learning (Berniker & Kording, 2008; Shadmehr & Krakauer, 2008; Wolpert & Ghahramani, 2000; Wolpert, Goodbody, & Husain, 1998; Zago, McIntyre, Senot, & Lacquaniti, 2009).

Here we will focus on the motor control studies providing evidence for the functioning of the system of internal representation and body schema used for controlling multi-segment movements and interaction with the extrapersonal space, in particular during human locomotion. Internal representation and control of movement depends not only upon various proprioceptive (as well as vestibular and visual) inputs and interaction between them, but must also take account of the length of the limb segments, a variable that is independent of muscle lengths and joint angles (Gandevia, Refshauge, & Collins, 2002). How does the nervous system encode specific body dimensions and adapt to a continuous body growth during development? This paper will describe and evaluate the results of recent research on the role of body proportions in determining the limb kinematics and estimating self-motion. First, we will underline in the following sections the role of central mechanisms for posture and movement regulation based on the internal model of the body. Then we will consider the dynamic processing of proprioceptive information for movement perception. Finally, we will address the role of body schema related information in multi-joint limb motion during human locomotion.

2. The role of perception for action

Although only a small part of human motor activity is reflected at the conscious level (Castiello, Paulignan, & Jeannerod, 1991; Fourneret & Jeannerod, 1998; Goodale, Milner, Jakobson, & Carey, 1991), motor and sensory components of action are deeply intertwined (Rizzolatti & Sinigaglia, 2007), suggesting inherent linkage between perception and action in the system of internal representation. Perhaps one of the most striking illustrations of the existence of the body schema is the modulation of spatially-oriented postural automatic responses evoked by changes in the internal

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