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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

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; Fournieret & 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

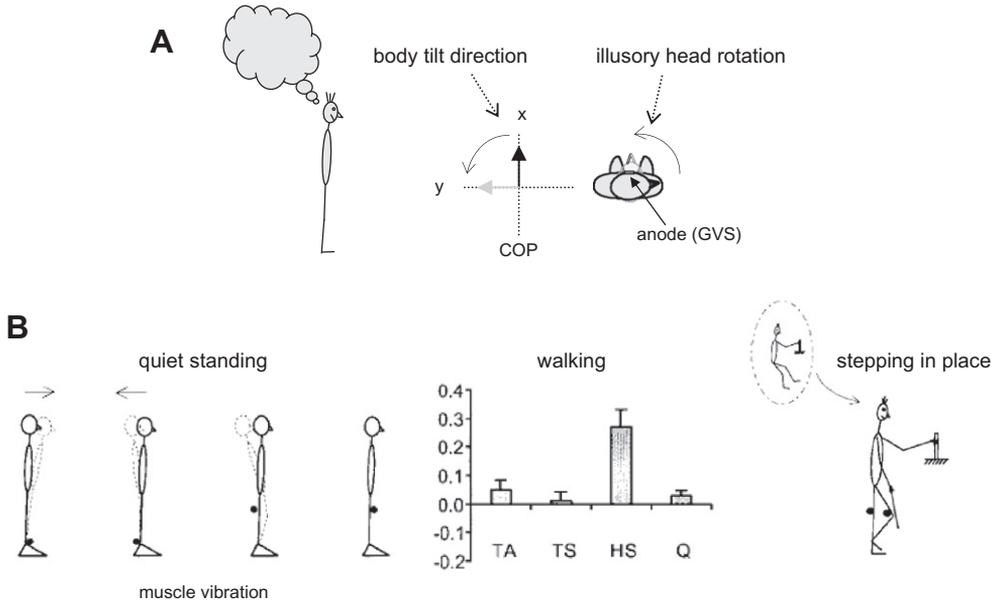


Fig. 1. Body schema related processing of sensory information. (A) Schematic illustration of the direction of postural responses to galvanic vestibular stimulation (GVS) induced by illusory changes of the head-on-foot orientation (Gurfinkel, Popov, Smetanin, & Shlykov, 1989). When the head is turned 90° to the right, postural body sway (center of pressure displacement) occurs perpendicular to the head-on-foot orientation (in the direction of anode, forward). However, when the subject experienced illusory return of the head to its neutral position, postural responses are reoriented accordingly (perpendicular to the perceived rather than actual head-on-foot orientation). (B) Task-dependent effects of proprioceptive stimulation. (Left panel) Schematic change of the body configuration in response to continuous muscle vibration during quiet standing. TA, tibialis anterior; TS, triceps surae; HS, hamstring; Q, quadriceps. Middle panel – walking speed increments during leg muscle vibration. Note a prominent speed increment in response to HS vibration. Right panel – illusory foot-on-trunk forward displacements induced by continuous HS muscle vibration during stepping in place (adapted from Ivanenko, Grasso, and Lacquaniti (Journal of Neurophysiology, 2000), with permission).

perception of body configuration. For instance, there are several techniques to artificially evoke a dissociation between real and perceived head-on-trunk orientation (Gurfinkel, 1994): by evoking proprioceptive illusions, by using the phenomenon of “return” of subjective head position to the middle (neutral) position after its prolonged turning, and by hypnotic suggestion. All these techniques demonstrate similar effects on postural responses to sensory stimulation (Gurfinkel, 1994). Fig. 1A illustrates a typical example of coupling between the perceived head-on-foot orientation and the direction of the body sway elicited by galvanic vestibular stimulation during quiet standing. Both change in parallel. Similar influences on the direction of postural responses can be elicited by changes in the direction of gaze, which may represent an important reference frame for the internal model of self-motion and spatial orientation (Ivanenko, Grasso, & Lacquaniti, 1999). Thus, the fact that the automatic responses are executed on the grounds of an illusory position of the limb (Gurfinkel, Ivanenko, & Levik, 1995; Gurfinkel, Popov, Smetanin, & Shlykov, 1989; Popov, Smetanin, Gurfinkel, Kudinova, & Shlykov, 1986; Smetanin, Popov, Gurfinkel, & Shlykov, 1988) indicates that the internal model does not only serve for conscious perception of position but is also the basis for planning and realization of motor activity.

3. Task-dependent processing of proprioceptive information

A wide spectrum of postural and movement tasks can hardly be accomplished by a simple control system based exclusively on reflex reactions. Furthermore, it is generally accepted that the processing

of proprioceptive information is context-dependent, and this evidence is briefly reviewed below. Proprioceptive reflexes may change within a motor task and between motor tasks, implying that the organizing structures and mono- and polysynaptic connectivity should be flexible (Stuart, 2002; Windhorst, 2007). In principle, such flexibility could be afforded by varying fusimotor actions and/or presynaptic inhibition. A classic example is gating and reversal of reflexes in ankle muscles during human stance and gait (Duysens, Trippel, Horstmann, & Dietz, 1990) or a reversal of the stretch reflex in human arm muscles during a catching task based on an internal model of limb geometry (Lacquaniti, Borghese, & Carrozzo, 1992). Postural instability represents another illustration of a profound reorganization of processing of proprioceptive information (Ivanenko, Talis, & Kazennikov, 1999; Solopova, Kazennikov, Deniskina, Levik, & Ivanenko, 2003). Task-dependent influences of proprioceptive stimulation during standing and walking are pointed out in Fig. 1B: in normal standing, distal muscle vibration (which activates predominantly Ia afferents of muscle spindles, Bianconi and van der Meulen (1963), Burke, Hagbarth, Lofstedt, and Wallin (1976) and Roll and Vedel (1982)) elicits a prominent body tilt, whereas during walking it has little if any effect (Courtine, Pozzo, Lucas, & Schieppati, 2001; Ivanenko, Grasso, & Lacquaniti, 2000). In contrast, during walking, proximal leg muscle (hamstring) vibration may evoke increments in walking speed (Ivanenko et al., 2000).

The organization of the interneuronal network and the use of corrective reactions points toward a rule-based control system rather than a simple additive principle of multisensory fusion (Misiaszek, 2006; Prochazka, 1996). Movement representations are often based on a priori knowledge about the dynamics of motion and predicted sensory consequences of the action (Ivanenko, Grasso, Israël, & Berthoz, 1997; McIntyre, Zago, Berthoz, & Lacquaniti, 2001). Reconstructing trajectory in space does not imply a mathematically perfect transformation of the linear and angular motion-related inputs into a Cartesian or polar 2D representation. Instead, physiological constraints on the interaction between motion direction and change of heading play an important role in motion perception (Ivanenko et al., 1997). Visual cues alone are insufficient to predict the time and place of interception or avoidance, and they need to be supplemented by prior knowledge (or internal models) about several features of the dynamic interaction with the moving object (Zago et al., 2009).

In fact, the usage of proprioception may differ significantly in static and dynamic conditions, since in dynamic conditions the control system applies some rules that are context-dependent (Bullen & Brunt, 1986; Capaday & Cooke, 1981; Cordo, Gurfinkel, Bevan, & Kerr, 1995; Inglis, Frank, & Inglis, 1991; Ivanenko et al., 1999, 2000; Viviani & Stucchi, 1989). For instance, during movement, the sensitivity of the spindle receptors in the shortening muscles is decreased and the information concerning limb position during movement comes primarily from the lengthening muscles (Capaday & Cooke, 1981). Stimulation of proprioceptors of the hamstring muscle may evoke illusory changes in the foot-on-trunk orientation during stepping in place (Fig. 1B, right panel) but not during quiet standing (Ivanenko et al., 2000). In sum, the sensory input coming from various proprioceptive channels is processed differently in static and dynamic conditions. An important example of the dynamic processing of proprioceptive information related to the central representation of limb kinematics and body dimensions is considered below.

4. Locomotor body schema

Body dimensions have to be taken into consideration by the CNS for planning locomotor movements and progressively updating information on the ongoing path while walking. The distance is often not directly available, e.g., when it cannot be inferred from a salient, reliable landmark or due to occlusion of the goal or distracted visual attention or when visual feedback is degraded (darkness, fog, etc.). The performance of a navigation task may be mediated by “path integration” that relies on self-motion cues to track distance and direction (Berthoz & Viaud-Delmon, 1999; Etienne & Jeffery, 2004; Loomis, Klatzky, & Golledge, 2001; Mittelstaedt & Mittelstaedt, 1980). Several studies indicate a major contribution of a step integrator or pedometer, rather than inertial cues or energy consumption related parameters (Glasauer, Amorim, Vitte, & Berthoz, 1994; Mittelstaedt & Mittelstaedt, 2001). For instance, ants with elongated (stilts) or shortened (stumps) legs take larger or shorter strides, respectively, and concomitantly misgauge travel distance (Wittlinger, Wehner, & Wolf, 2006). In principle, a

step integrator and a time-lapse integrator would both yield the same homing distances if the walking speed were kept constant (Glasauer, Schneider, Grasso, & Ivanenko, 2007), however, the step length and stepping frequency need to be taken into account in the estimation of the walking speed. Moreover, how is sensory information dynamically processed to estimate step length and walking distance?

Recently, we investigated the role played by implicit knowledge of body dimensions in locomotion and computation of distance walked when changes in body size are acquired artificially, following a non-developmental pattern (Dominici et al., 2009). For this purpose, we analyzed recovery of locomotion and walking to a memorized target in an achondroplastic (ACH) 10-year child who underwent progressive surgical elongation of the shank segment using the Iliazorov technique (Cattaneo, Villa,

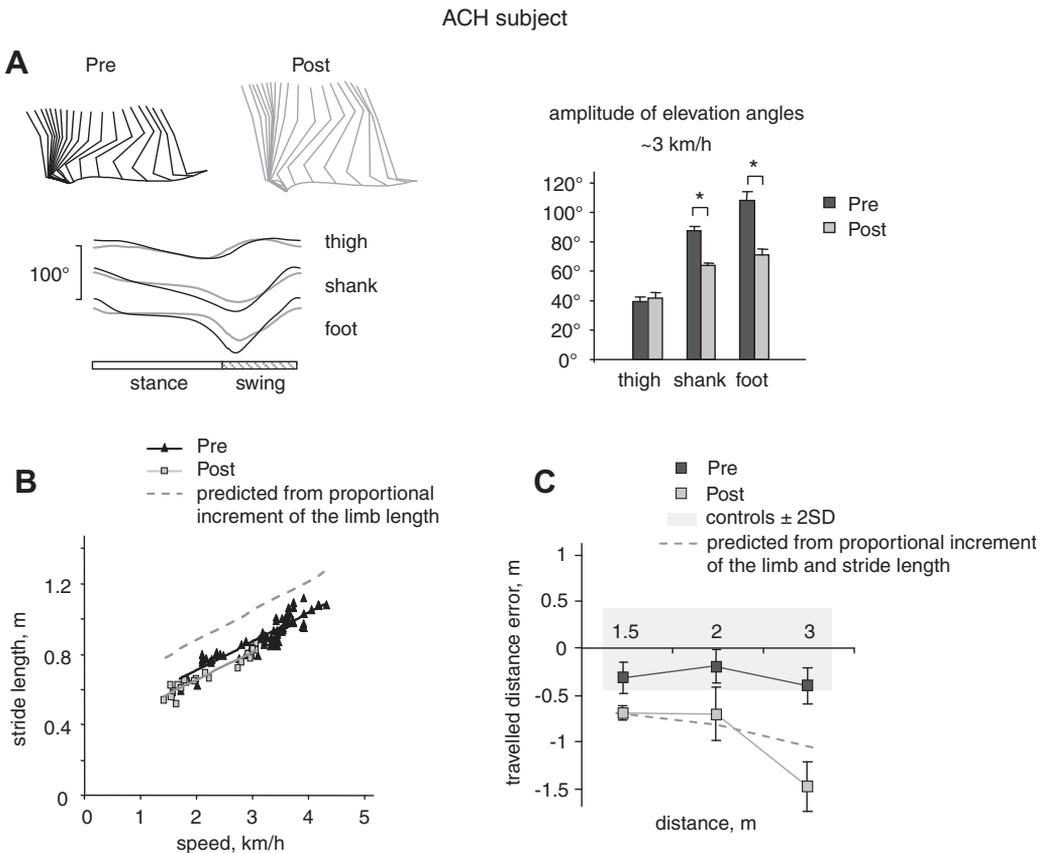


Fig. 2. Locomotor patterns and walking distance estimation in the ACH subject before and after shank elongation. (A) Changes in the kinematic pattern. (Left panel) Stick diagrams and ensemble averaged segment elevation angles (relative to the vertical) during walking at about the same speed (~3 km/h) in the pre and post sessions. The thigh, shank and foot elevation angles are positive in the forward direction, i.e., when the distal marker falls anterior to the proximal one. (Right panel) peak-to-peak amplitudes (+SD) of angular motion. Asterisks denote significant differences. (B) Changes in the stride length as a function of walking speed (each point corresponds to one individual stride). Changes with speed are fitted by a linear function. Note similar (even slightly shorter) stride length in the post session despite drastic elongation of the limb. The dashed line represents the expected modification in the stride length attributable to normal development. (C) Travelled distance errors while walking with eyes closed towards a memorized target located at three distances: 1.5, 2, and 3 m. The error was calculated as the difference between the required and actual distance performed by the ACH child. Negative error represents smaller travel distances. The dashed line represents the error predicted from the proportional increment of the limb and stride length, relative to the performance before limb elongation. The grey area corresponds to the range (2SD) of travelled distance errors in age-matched typically developing children. Adapted from Dominici et al. (*Journal of Neurophysiology*, 2009) with permission.

Catagni, & Tentori, 1988; Ilizarov & Deviatov, 1971). The whole surgical procedure of shank elongation lasted 13 months and resulted in an increased length of both shank segments by 22 cm, while length of other body segments remained unvaried. The child was tested 3 months before (pre) and 3 months after elongation was completed (post). In addition, we investigated task performance in adults walking on specially designed stilts imitating limb segment proportions in ACH.

Fig. 2 illustrates the main findings of this study. First, the inter-segmental coordination in ACH changed markedly following limb elongation, presumably as a result of biomechanical constraints, i.e., larger inertia and length of the shank segments. Prominent modifications occurred in the relative changes of angular segment motion: the distal segments (shank and foot) showed much less oscillations relative to the pre-elongation gait while the proximal thigh segment displayed comparable oscillations (Fig. 2A). Based on values recorded from a population of typically developing individuals one would expect lengths of ACH strides to be about 17 cm longer than before elongation (Fig. 2B, dashed line). However, despite total limb length increased of ~50% with the shank elongation, the child maintained his step length almost unvaried (Fig. 2B) when walking at comparable speeds.

The lack of variation in step length between the two sessions paradoxically resulted in shorter walking paths to a memorized target (Fig. 2C). It is worth noting that proprioception, as clinically assessed post-surgery, was not affected, suggesting that this subject could adequately benefit from this information in both sessions. A possible explanation for the reported error could be that the shorter walking distances recorded after surgery resulted from the slower walking speeds adopted, an adaptive behavior that is common in other patient populations. However, this mechanism is unlikely to account for shorter paths since speed-related influences on path integration are small (Glasauer et al.,

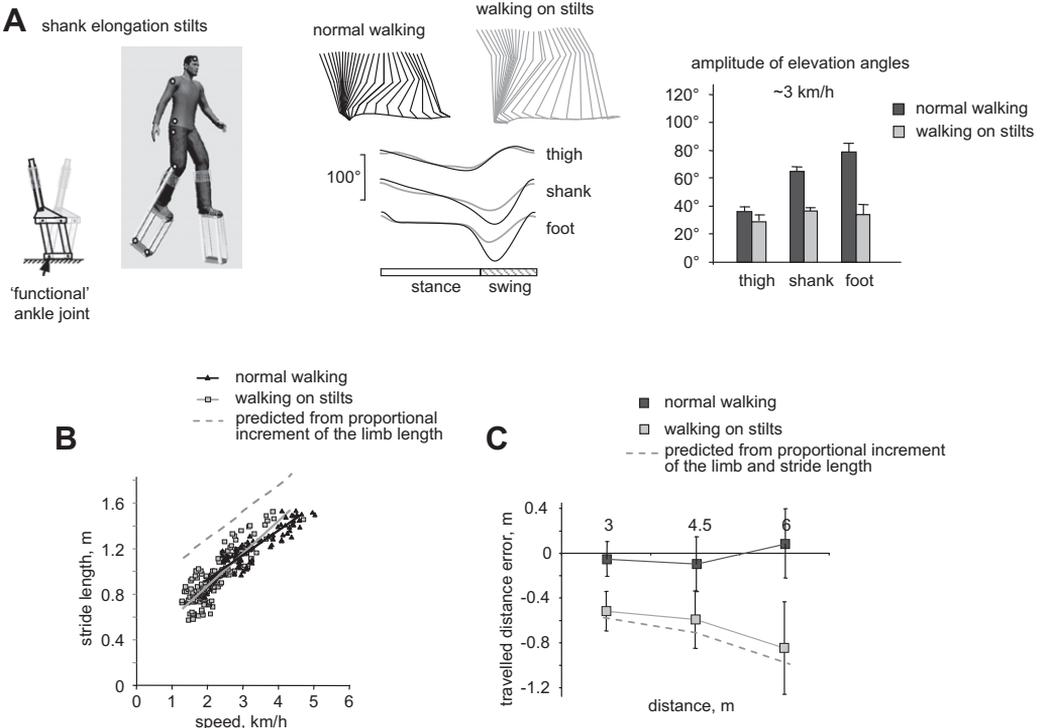


Fig. 3. Locomotor patterns and walking distance estimation in adults during walking on the specially designed stilts imitating shank elongation. The same format as in Fig. 2 except for panel C. Shank segment elongation was imitated by attaching a rotational parallelepiped-like support of the height $h = 42$ cm so that the functional axis of ankle rotation was displaced downwards to a distal part of the stilts. Adapted from Dominici et al. (*Journal of Neurophysiology*, 2009) with permission.

1994) and, more important, slower walking speeds typically give rise to larger (rather than shorter) travel distances in normal individuals (Bredin, Kerlirzin, & Israël, 2005; Mittelstaedt & Mittelstaedt, 2001). Therefore, we suggest that the unusual locomotor distance estimation after elongation could depend on the interfering effect produced by changes in the limb kinematics and may be caused by an “erroneous” limb movement and step length representation.

Moreover, even though walking on stilts (Fig. 3A) can only partially imitate physiological consequences of shank elongation in ACH (e.g., the actual muscle lengths were not changed), the results in adults wearing stilts (Fig. 3) were strikingly similar, suggesting a strong relationship between intrinsic limb dynamics and walking distance perception (Dominici et al., 2009). Disproportional lengthening of the lower limbs had parallel consequences on both step length (see also Noble, Singer, & Prentice, 2009) and distance estimation (Figs. 2 and 3). In fact, the differences between actual stride length and the length of the foot path expected from “normal” proportional lengthening of the limb in typically developing individuals could well account for the observed walking distance negative errors (Figs. 2 and 3, dashed lines). For instance, the CNS may take into account just the hip angle oscillations (which do not change substantially after shank elongation, Figs. 2A and 3A) and use them for estimating the stride length according to a priori knowledge about the relationship between the limb length, leg aperture (hip angle oscillations) and stride length (Grieve & Gear, 1966). This implies a dissociation between actual disproportional body schema and proportional dynamic body image. It is also worth noting that all subjects were aware of their increased (by ~50%) “static” limb length. Thus, the reason for the observed perceptual phenomenon may reside in the dynamic nature of proprioceptive information processing.

The incomplete adaptation to modified limb proportions seems at odds with previous studies showing that somatotopic maps from the receptors to the cortex are not fixed but can be altered by experience (Di Russo et al., 2006; Flor et al., 1995; Merzenich & Jenkins, 1993; Ramachandran, Rogers-Ramachandran, & Stewart, 1992). Moreover, the body schema in primates may incorporate external objects or tools (Berti & Frassinetti, 2000; Iriki, Tanaka, & Iwamura, 1996; Ivanenko, Grasso, Macellari, & Lacquaniti, 2002; Ivanenko, Levik, Talis, & Gurfinkel, 1997; Lacquaniti, Soechting, & Terzuolo, 1982) expanding a central representation of the limb endpoint and resulting in a “functional” elongation of the limb. Therefore, one could in theory expect rapid adaptation of motor performance

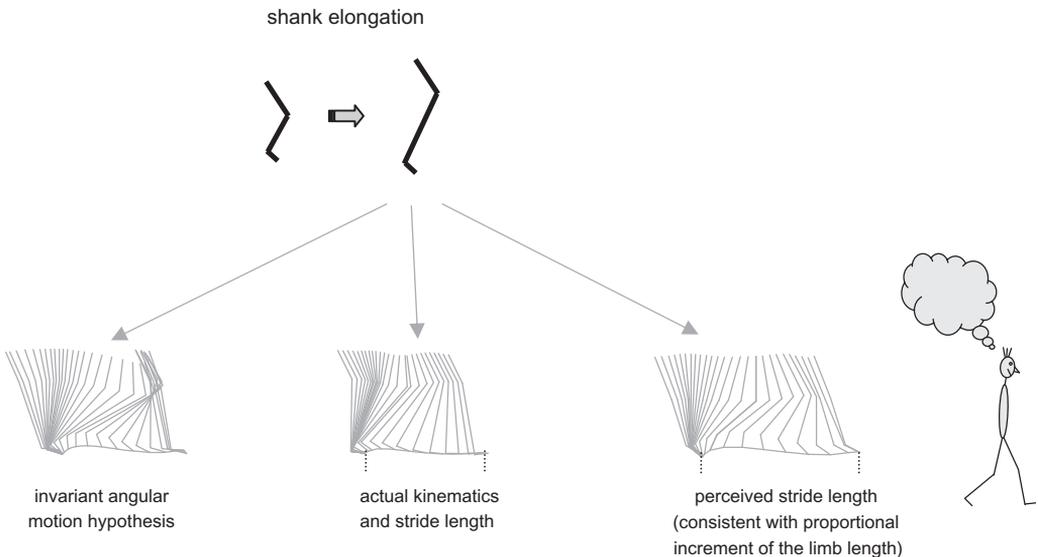


Fig. 4. Hypothetical “conservative” locomotor body schema for step length estimation revealed by kinematic and perceptual changes after shank segment elongation. (Left) Stick diagram of one simulated gait cycle under the assumption of invariant joint angle movements (same as before elongation). (Middle panel) Actual recorded kinematics. (Right panel) Internal representation of the gait kinematics and stride length consistent with the proportional increment of the limb length.

to progressively elongated shank segments in the ACH subject or normal adults walking on stilts. The inconsistency could be explained by several considerations: first, adaptation might require longer experience than that offered in the present study, especially taking into account that we are much less habituated for using a “tool” with the foot than with the hand. For instance, experienced stilt users (daily stilt use for >6 years) show less reduction in step length, while the novice group demonstrated a more cautious walking strategy (Noble et al., 2009). Second, no visual feedback was allowed in the present case, thus possibly preventing learning. Besides, using a tool might differ both functionally and neurophysiologically from changing our own body dimensions. For instance, we can estimate the weight of an external object in the hand but we cannot tell exactly what the weight of our own hand is. The same analogy could possibly be valid for body representation. We can incorporate a tool (Maravita & Iriki, 2004) or a support (Pearson & Gramlich, 2010; Solopova et al., 2003) into our postural body schema, but our own limb proportions and self-motion representations can be “conservative”, at least as far as it concerns predicted sensory consequences of the action (Ivanenko et al., 1997; McIntyre et al., 2001).

We do not know how sensory information is dynamically processed to estimate step length. For example, populations of spinocerebellar neurons provide information to the cerebellum about foot motion (Poppele & Bosco, 2003) and, apparently, segment length proportions and the dynamic properties of muscle spindle firing should be implicitly involved in these computations. Our results (Dominici et al., 2009) are consistent with the “conservative” locomotor body schema revealed by the subjective reports on travelled distance. Fig. 4 illustrates the conceptual framework for estimating the step length in humans. Given the disproportional lengthening of the limb length, one would expect to detect major changes in the locomotor pattern after elongation. Indeed, maintaining the same joint angle motion would be infeasible since this would result in unrealistic anterior–posterior and vertical hip displacements (see simulation results in Fig. 4, left panel, in particular – the end of the swing phase), that would even be entirely unmatched on the contralateral side resulting in absurd trunk deformations. Therefore, the control system must adapt to the new limb proportions. In fact, all subjects were able to do it. This kinematic adaptation is interesting *per se* and may shed light on optimization of human body proportions and the evolution of *Homo* (Rolian, Lieberman, Hamill, Scott, & Werbel, 2009). Nevertheless, our findings support the hypothesis of an intermediate form of adaptation. Namely, while biomechanical adaptations appear to have occurred for the purpose of locomotion, proper knowledge of the change had not been available for distance estimation. In fact, ACH and normal adults walking on stilts behaved as if they overestimated the actual step length and distance travelled consistent with proportional increment of the limb length (Fig. 4, right diagram). This “conservative” dynamic body schema may be based on inherent relationships between gait parameters and evolutionary adopted body proportions.

5. Concluding remarks

The fact that shank elongation evoked parallel changes in the limb kinematics and travelled distance estimation may suggest the existence of a locomotor body schema used for controlling step length and path estimation. This locomotor body schema comes from a sort of interplay between a priori notions about inherent dynamics of multi-joint limb motion and proprioception. We may marvel looking at artistic works on human body, such as the Apollo and Daphne by Bernini or the Vitruvian Man by Leonardo da Vinci. However, why do we have such body proportions? Apparently, they result from optimization and a long history of the evolution of *Homo*. In fact, the way in which the locomotor body schema and gait kinematics are optimized and encoded centrally in different animals represents a fascinating area of research (Alexander, 1989; Ivanenko, Cappellini, Dominici, Poppele, & Lacquaniti, 2007; Poppele & Bosco, 2003; Rolian et al., 2009; Saibene & Minetti, 2003).

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