Modulation of spinal excitability during observation of bipedal locomotion

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This study investigated whether a mirror mechanism exists for bipedal locomotion. We employed the soleus (plantar flexor) Hoffman reflex to investigate corticospinal excitability at the spinal level during observation of bipedal locomotion. The differential amplitude modulation of the left soleus Hoffman reflex during observation of bipedal heel-stepping (plantar dorsiflexion) ($324 \pm 53\,\mu V$), standing still ($383 \pm 60\,\mu V$), and bipedal toe-stepping (plantar flexion) ($419 \pm 53\,\mu V$) reached significance ($P < 0.05$). The observation of bipedal toe-stepping produced a greater increase in spinal excitability than the observation of bipedal heel-stepping. These findings support the suggestion that there is a mirror mechanism for bipedal locomotion and they demonstrate that spinal excitability for observation of bipedal locomotion mirrors that for execution of bipedal locomotion. *NeuroReport* 16:1711–1714 © 2005 Lippincott Williams & Wilkins.

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Introduction

Humans can recognize the different forms of bipedal locomotion accurately and robustly [1]. On the basis of point-light displays, walking and running can be immediately recognized [2]. These phenomena suggest that during the observation of locomotion, some sort of motor resonance is likely to occur in the observer. Empirical evidence supporting the existence of mirror mechanisms, however, is mainly drawn from studies involving mouth, hand, and foot actions [3–9]. To our knowledge, no study addresses whether there is a mirror mechanism for bipedal locomotion. The current experiment assesses spinal excitability during the observation of bipedal locomotion on the basis of previous studies of spinal excitability during the observation of hand actions. While humans observe hand actions, spinal excitability measured by the cervical Hoffman reflex (H-reflex) related to the right finger flexor [8] showed a contrast with the cortical excitability evoked by transcranial magnetic stimulation over the premotor cortex [9]. Cortical excitability was a mirror pattern that replicated the observed hand actions whereas spinal excitability was an inverted mirror pattern that, it was suggested, prevented the overt replication of the observed hand actions. The present study investigates whether there is a mirror mechanism for bipedal locomotion at the spinal level. As bipedal locomotion works in a manner conforming to bipedal step [10], spinal excitability during the observation of bipedal step could be conceivably linked to that of bipedal locomotion. We postulate that the observation of bipedal step and standing still produce different amplitude modulation of the soleus (plantar flexor) H-reflex, on each side.

Materials and methods

General procedures

Human subjects participated in the study after giving written, informed consent. The study was approved by the local Ethics Committee and conducted in accordance with the Declaration of Helsinki. All participants were right handed and right foot dominant according to the Edinburgh handedness inventory [11]. No study participant had any neurological, psychiatric, or medical disorder. Participants lay comfortably prone on a physical examination bed with their eyes at about 50 cm distance from a 14-inch LCD screen. Their feet were hung over, with the lateral malleolus approximately at the posterior rim of the bed.

Constant current pulses (duration 0.5 ms) were delivered (DANTEC, Skovlunde, Denmark) to evoke the monosynaptic soleus H-reflex on each leg. The bipolar surface-stimulating electrode was positioned over the posterior tibial nerve near the center of the popliteal crease under constant fixation. The recording electrode was positioned on the soleus muscle, halfway between the midpoint of the popliteal fossa and the upper border of the medial malleolus. The reference electrode was placed in the same line 5 cm distal to the active electrode, and the ground electrode was placed between the stimulating and reference electrodes. The stimulating electrodes were correctly positioned by inspecting muscle twitch stimulation. The stimulation frequency was around 1 Hz to avoid the habituation phenomenon [12]. The stimulus intensity was increased until maximal H-reflex amplitude and minimum motor response (M-wave) were reached, while the participant lay prone, facing the black screen. The mean amplitude of five elicited H-reflexes in this condition was the *baseline*, which showed no significant difference between left and right legs. Given this stimulus intensity at the *baseline*, the test H-reflex responses on each leg were elicited immediately following the commencement of each video presentation. During video presentation, participants were requested to keep still and watch what was presented on the screen attentively. The order of stimulation of the legs (left and right) was randomized and counterbalanced. In order to assess the absence of any spontaneous electromyography (EMG) activity during video presentation, pre-trigger background EMG (5 s) was acquired before H-reflex stimulation. No EMG activity was found in the rectified background traces.

The video presentation included a randomized sequence of four videos (video duration, 5 s) representing (1) standing still, *stand*; (2) bipedal stepping, *step*; (3) bipedal toe-stepping, *toe*; and (4) bipedal heel-stepping, *heel*. *Stand* was used as a control. *Step* represented bipedal locomotion. *Toe* and *heel* presented movements during which the soleus muscle acts as an agonist and antagonist, respectively. A male with right dominant foot acted in the video clips depicting bilateral lower legs.

During presentation of each condition (*step*, *stand*, *toe*, *heel*), five H-reflexes were elicited separately on each leg. Peak-to-peak amplitudes of the H-reflex were measured. Then, the amplitude modulation of the H-reflex at each condition was defined as the difference (in microvolts) by subtracting the averaged H-reflex amplitude from the *baseline*.

Experiment 1

Fifty-four healthy participants (26 males and 28 females; mean age 25 years) were shown the four videos (*step*, *stand*, *toe*, *heel*) filmed from the actor's left side in lateral view. Then, the statistical analysis using a paired t-test compared the amplitude modulation of each condition between the right and left legs. A two-way repeated-measures ANOVA [leg (left, right) × bipedal (*step*, *stand*)] examined the existence of a mirror mechanism for bipedal locomotion. Two-way repeated-measures ANOVA [leg (left, right) × bipedal (*toe*, *heel*, *stand*)] followed by post-hoc tests examined spinal excitability across observation of different types of bipedal locomotion. The H-reflex amplitude modulation at each condition was displayed as mean ± SEM. The significance level was set at $P<0.05$.

Experiment 2

Four healthy participants (two males and two females; mean age 24 years) underwent the same paradigm, except that the videos (*step*, *stand*, *toe*, *heel*) were filmed from the actor's right side in lateral view. Then, the H-reflex amplitude modulation at each condition was displayed as mean ± SEM.

Results

Experiment 1

Left versus right legs

The H-reflex amplitude modulation during *step*, *stand*, *toe*, and *heel* was 341 ± 60, 383 ± 60, 419 ± 53, and 324 ± 53 μV, respectively, on the left leg and 232 ± 50, 118 ± 74, 264 ± 61, and 262 ± 52 μV, respectively, on the right leg. The left leg showed greater amplitude modulation than the right leg regardless of which type of bipedal locomotion the participant was observing (*step*, $P>0.05$; *stand*, $P=0.01$; *toe*, $P=0.05$; *heel*, $P>0.05$).

Observation of step

No main effect was observed in bipedal locomotion (*step*, *stand*), but a main effect was found in the leg (left, right) ($P=0.02$) and in the interaction ($P=0.04$). *Step* has similar amplitude modulation ($P>0.05$) between the right and left legs whereas *stand* has significantly different amplitude modulation between the right and left legs ($P<0.05$) (Fig. 1).

Observation of toe and heel

Figure 2 illustrates the H-reflex and M-wave during *baseline*, *heel*, *stand*, and *toe* in one participant. For a total of 54 participants, there were main effects in the leg (left, right) ($P=0.02$) and in bipedal locomotion (*toe*, *heel*, *stand*) ($P=0.03$), as well as in their interaction ($P=0.03$). After post-hoc examination, there was a significant difference between *toe* and *stand* ($P=0.01$). Neither the difference between *toe* and *heel* nor the difference between *heel* and *stand* observation reached significance. Figure 3 demonstrates the expression of spinal excitability during observa-

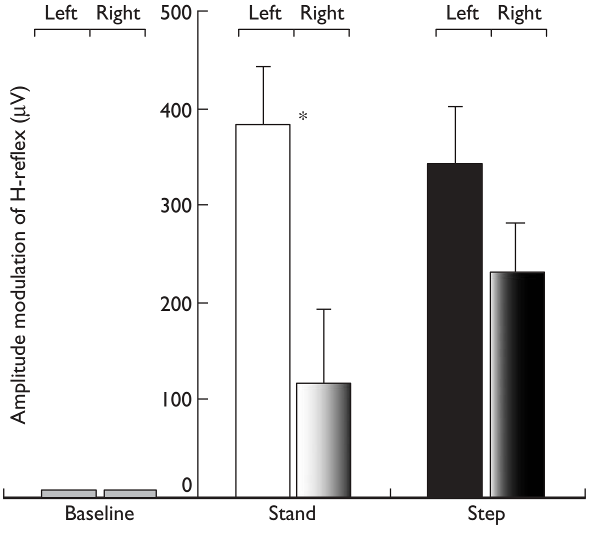

Fig. 1 Amplitude modulation of the Hoffman reflex (H-reflex) relative to the *baseline* during *step* and *stand*. Significant interaction ($P=0.04$) was found between the leg (left, right) and bipedal locomotion (*step*, *stand*). *Step* had similar amplitude modulation ($P=0.14$) between the left and right legs but *stand* had significant different amplitude modulation between the left and right legs ($P=0.01$,*). Such a discordant pattern underscores the presence of a human mirror mechanism at the spinal level for bipedal locomotion.

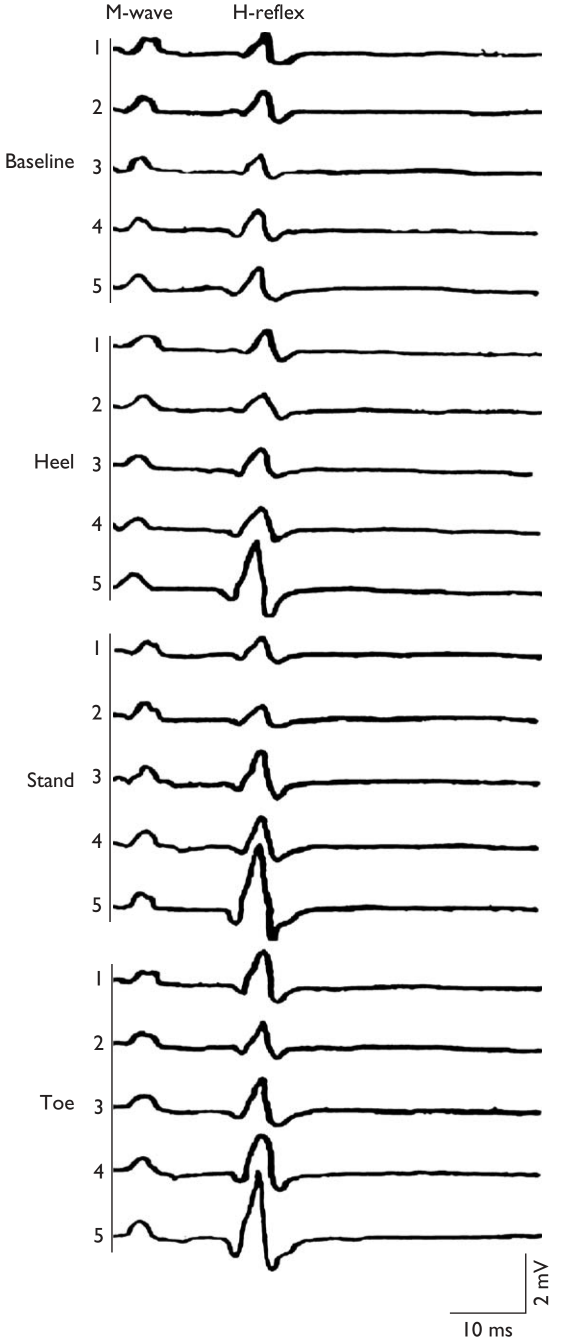

Fig. 2 M-wave and Hoffman reflex (H-reflex) responses of the left leg during *baseline* and *heel*, *stand*, and *toe* in one participant. *Heel*, *stand*, and *toe*, respectively, show a similar M-wave to the *baseline*; but each of them displays different amplitudes of H-reflex from the *baseline*. While the actual contraction of the soleus muscle increases from *heel*, *stand* to *toe*, the amplitude of the H-reflex increases during their observation accordingly.

tion of bipedal locomotion as a mirror pattern. While the actual contraction of the soleus muscle increases from *heel*, *stand* to *toe*, the amplitude modulation of the left soleus H-reflex during their observation increases accordingly (Fig. 3a). During observation from the actor's left side, the left leg displayed a mirror pattern more prominently than the right leg.

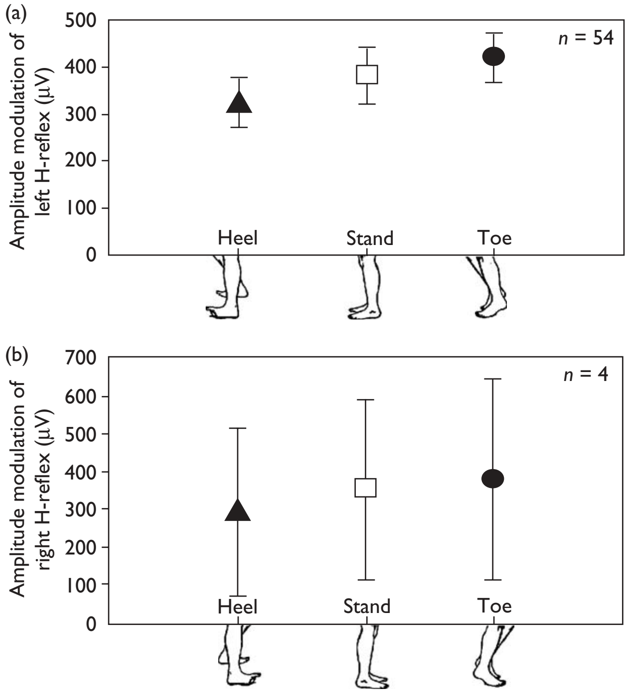

Fig. 3 Observation of bipedal locomotion mirrors execution of bipedal locomotion at the spinal level. The soleus muscle acts as an agonist and antagonist in executing *toe* and *heel*, respectively. *Stand* was used as a control. The expression of spinal excitability during observation of *heel*, *stand*, and *toe* expressed a scenario as a mirror pattern. (a) Amplitude modulation of left soleus Hoffman reflex (H-reflex) during observation of bipedal locomotion from the actor's left side in lateral view in accordance with actual contraction of the soleus muscle. While the actual contraction of the soleus muscle increases from *heel*, *stand* to *toe*, the amplitude modulation of the left soleus H-reflex increased accordingly. Data from 54 participants were averaged. (b) Amplitude modulation of right soleus H-reflex during observation of bipedal locomotion from the actor's right side in lateral view in accordance with actual contraction of the soleus muscle. While the actual contraction of the soleus muscle increases from *heel*, *stand* to *toe*, the amplitude modulation of right soleus H-reflex tended to increase accordingly. Data from four participants were averaged. The left leg expressed spinal excitability as a mirror pattern during observation of bipedal locomotion from the actor's left side whereas the right leg tended to express that during observation of bipedal locomotion from the actor's right side. Error bars indicate SEM.

Experiment 2

The H-reflex amplitude modulation during *step*, *stand*, *toe*, and *heel* was 238 ± 377, 435 ± 263, 352 ± 313, and $484 \pm 440\,\mu V$, respectively, on the left leg and 522 ± 335, 354 ± 235, 379 ± 261, and $296 \pm 221\,\mu V$, respectively, on the right leg. During observation from the actor's right side, spinal excitability of the right leg tends to express a mirror pattern (Fig. 3b).

Discussion

The current study demonstrated that, in the absence of any detectable muscle activity, the mere observation of *step* differed from that of *stand* in the observer's spinal excitability. This result lends support to the existence of a mirror mechanism for bipedal locomotion. It is worth noting that spinal excitability during the observation of bipedal locomotion showed a mirror pattern, contrary to an inverted mirror pattern seen during the observation of hand actions. Furthermore, asymmetrical amplitude modulation was found between the left and right legs. The left leg showed a mirror pattern during observation from the actor's left side.

It is interesting to note that spinal excitability during the observation of bipedal locomotion here differs from the result of a previous study during the observation of hand actions [8]. That study reported that the H-reflexes of the finger flexors are facilitated during observation of hand opening (finger extension) and inhibited during observation of hand closure (finger flexion). On the contrary, our study shows that the H-reflex of the plantar flexors (soleus muscle) is inhibited during the observation of *heel* (plantar dorsiflexion) and facilitated during the observation of *toe* (plantar flexion). The discrepancies between these two studies could be ascribed to the dynamics of the human mirror mechanism that operates with a profile from inverted mirror patterns to mirror patterns at the spinal level. The wide range of spinal excitability may have a lead-in effect on the likelihood of an observed action being reproduced by the observer [13]. Selective facilitation and inhibition can occur at segmental spinal levels during motor imagery, and probably during action perception as well [14]. Some contagious human behaviors, like laughing and yawning, may have instant facilitation or disinhibition of the perceiver's corresponding brain or spinal circuits to prompt replication of the seen actions, whereas other behaviors may be resistive to excitation or to the overdriving inhibition to prohibit overt replica of the seen actions. In fact, body parts may express themselves differently to various levels of transmission of motor representation. Whereas spinal excitability changed insignificantly during simulated wrist movements [15], it changed significantly during mentally simulated isometric foot exertion [16]. Thus, it is conceivable that spinal excitability of the human mirror mechanism suggests the likelihood of an observed action being repeated by the observer.

Moreover, asymmetrical amplitude modulation between the left and right legs might result from the observation of bipedal locomotion in lateral view. The video presentation from the actor's left side yielding a more prominent image of the left leg facilitated the expression of spinal excitability as a mirror pattern on the left leg. *Experiment 2*, with a small number of participants also demonstrated that the video presentation from the actor's right side yielding a more prominent image of the right leg tended to express spinal excitability as a mirror pattern on the right leg. Aziz-Zadeh *et al.* [17] reported that the motor-evoked potentials were larger while participants were observing the hand actions with transcranial magnetic stimulation concurrently applied to the contralateral motor cortex. The contralateral preponderance of the expressed excitability suggested a sensory–motor interaction, that is, sensory disposition (e.g. perspective of observation) may have a direct impact on spinal excitability even when no motor output is required.

Conclusion

Our study suggests there is a mirror mechanism for bipedal locomotion in humans. The spinal excitability for observation of bipedal locomotion mirrors that for execution of bipedal locomotion.

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