Neuroscience 155 (2008) 640–648

CAN PREPARED ANTICIPATORY POSTURAL ADJUSTMENTS BE UPDATED BY PROPRIOCEPTION?

H. RUGET,[a] J. BLOUIN,[a] N. TEASDALE[b] AND L. MOUCHNINO[a]*

[a]*Laboratoire Neurobiologie de la Cognition, Aix-Marseille Université, CNRS, Université de Provence, UMR 6155 case C, 3 place Victor Hugo, F-13331 Marseille cedex 3, France*

[b]*Groupe de Recherche en Analyse du Mouvement et Ergonomie, Université Laval, Faculté de Médecine, Division de Kinésiologie, PEPS, Québec, G1K 7P4 Québec, Canada*

Abstract—Stepping over an obstacle is preceded by a center of pressure (CoP) shift, termed anticipatory postural adjustments (APAs). It provides an acceleration of the center of mass forward and laterally prior to step initiation. The APAs are characterized in the lateral direction by a force exerted by the moving leg onto the ground, followed by an unloading of the stepping leg and completed by an adjustment corresponding to a slow CoP shift toward the supporting foot. While the importance of sensory information in the setting of the APAs is undisputed, it is currently unknown whether sensory information can also be used online to modify the feedforward command of the APAs. The purpose of this study was to investigate how the CNS modulates the APAs when a modification of proprioceptive information (Ia) occurs before or during the initiation of the stepping movement. We used the vibration of ankle muscles acting in the lateral direction to induce modification of the afferent inflow.

Subjects learned to step over an obstacle, eyes closed, in synchrony to a tone signal. When vibration was applied during the initiation of the APAs, no change in the early APAs was observed except in the case of a cutaneous stimulation (low frequency vibration); it is thus possible that the CNS relies less on proprioceptive information during this early phase. Only the final adjustment of the CoP seems to take into account the biased proprioceptive information. When vibration was applied well before the APAs onset, a postural reaction toward the side of the vibration was produced. When subjects voluntarily initiated a step after the postural reaction, the thrust amplitude was set according to the direction of the postural reaction. This suggests that the planned motor command of the APAs can be updated online before they are triggered.

Key words: postural control, vibration evoked-signal, somatosensory afferents, stepping over an obstacle.

The production of voluntary movements is generally accompanied by postural adjustments. In several cases, muscles responsible for these postural adjustments are activated before those acting as prime movers. For instance, step initiation is preceded by the coactivation of tibialis anterior (TA) and medial gastrocnemius muscles of the stepping leg. These activations generate sideward and backward displacements of the center of pressure (CoP), which in turn accelerates the center of mass (CoM) toward the supporting leg and forward (Robert et al., 2004). These postural adjustments are essential because they allow the unloading of the stepping leg and so create the necessary condition for progression (Brénière and Do, 1991). Starting before the step (but continuing during the movement), they are referred to as anticipatory postural adjustments (APAs) (Kaminski and Simpkins, 2001; Malouin and Richards, 2000; Massion, 1992; Timmann and Horak, 2001). Intracerebral recordings in the cat and lesion studies in humans have shown that the coordination between the APAs and the focal leg movement are organized at a supraspinal level and involve the pontomedullary reticular formation, the supplementary motor area and the basal ganglia (Massion et al., 1999; Viallet et al., 1992; Gantchev et al., 1996; Schepens and Drew, 2004). The APAs could be progressively assembled and stored in advance of movement and triggered by corticospinal excitations. MacKinnon et al. (2007) have shown that magnitude and duration of the APAs increased as a startle-like acoustic stimulus (which causes an early release of the planned movement) timing approach the "go" signal for step initiation. The scaling of the APAs before their dispatch to the periphery depends on the ability to use sensory information from various sources (vestibular, cutaneous, visual, proprioceptive) (Mille et al., 1998; Timmann and Horak, 1998). Studying step initiation in response to a backward surface translation (which moved the subjects' CoM forward off their base of support), Timmann and Horak (2001) found that sensory information was integrated rapidly to adjust the APAs. Indeed, the authors showed that although the stepping response had short reaction times (~200 ms), the APAs were well adapted to changes in body state introduced prior to movement onset. They suggested that proprioceptive inputs arising from such postural reactions in addition to activation of mechanoreceptors from the sole of the foot and also vestibular signals, could contribute to the re-setting of the planned motor command. These studies also suggest the APAs could be modulated by somatosensory information originating from the body movement. However, the movement was imposed before the APAs had been initiated. While the importance

---

*Corresponding author. Tel: +33-0-4-88-57-68-14; fax: +33-0-4-88-57-68-72.
E-mail address: laurence.mouchnino@univmed.fr (L. Mouchnino).
Abbreviations: ANOVA, analysis of variance; APAs, anticipatory postural adjustments; CoM, center of mass; CoP, center of pressure; EMG, electromyogram; GM, gastrocnemius medialis; GVS, galvanic vestibular stimulation; M/L, medio-lateral; PR, postural response; TA, tibialis anterior.

doi:10.1016/j.neuroscience.2008.06.021

of sensory information in the setting of the APAs is undisputed, it is currently unknown whether sensory information can also be used online to modify the feedforward command of the APAs.

The possibility of controlling the APAs during their execution has been investigated by Bent et al. (2002). The authors stimulated the vestibular apparatus of individuals for 7.5 s (using the galvanic vestibular stimulation (GVS) technique) starting 1.5 s before they started to walk straight-ahead with eyes closed. Despite GVS evoking a slight body tilt toward the anode side, the APAs (i.e. the lateral forces produced to unload the stepping leg) were unaffected by the change in the vestibular afferents. The effect of GVS was only identified at the start of the second step. This led to the suggestion that vestibular information has little influence on both the setting and the online control of the APAs, and that it only becomes relevant during the more dynamic control of the stepping task. In this experiment, we used muscular vibration techniques to investigate whether leg muscle proprioception is processed by the CNS to then control the APAs online, that is once they are initiated. The fact that proprioception-based movement corrections can have short latencies (<100 ms, i.e. shorter than for initiating movement through proprioceptive cues, Gomi et al., 2002; Ito et al., 2005) allows for such a possibility. If proprioceptive signals are used in the online control of the APAs, then erroneous vibration-induced detection of the current body state should be reflected in the APAs.

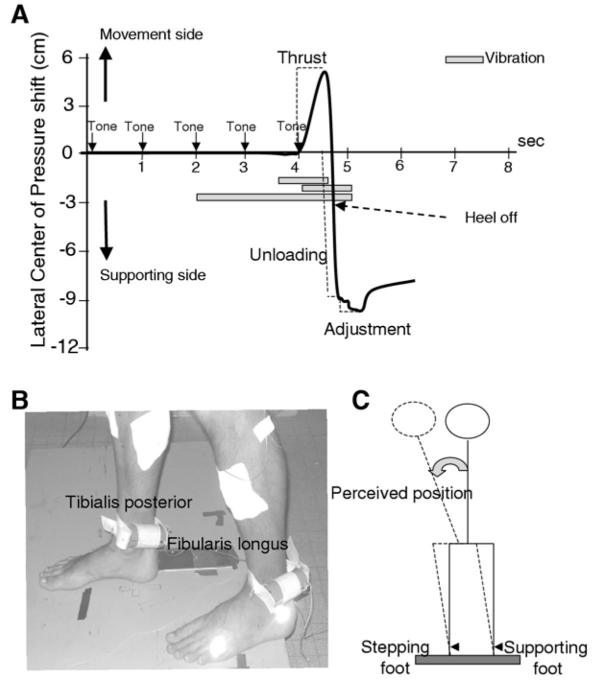

Fig. 1. (A) CoP lateral displacement during step avoidance task. After an initial displacement toward the stepping side (Thrust), the CoP moved toward the supporting side (Unloading and Adjustment). The dotted lines represent the onset and offset of each phases. The "heel off" indicates the onset of the stepping movement. Time 0 corresponds to the start of the data recordings, the vibration had been applied at different times during the preparation and APAs initiation. (B) Example of vibrators placement. (C) Illustration of the effect of the sensory message induced by vibration when the vibrators are placed as shown in B.

EXPERIMENTAL PROCEDURES

Subjects stood barefoot on a force platform. In the main experimental condition, they were asked to make a complete step over an obstacle (height: 23 cm×width: 45 cm×depth: 12 cm) with the right leg and to stop just beyond it. In order to generate the vibration at specific times with respect to APAs onset, subjects were asked to synchronize their step initiation with the fifth 1-s-interspaced tone produced by a computer (Fig. 1A). A few practice trials were required for the subject to comply with this requirement. The subjects' eyes were open, looking at the obstacle and then closed at the first tone. Eccentrically loaded motors inserted in plastic cylinders provided the vibration stimuli. The vibrators were securely fixed with an elastic belt, one vibrator on each leg, just above the external malleolus on the fibularis longus muscle and above the medial malleolus on the tibialis posterior muscle. With such arrangement, the vibrations acted on both the right-side of one leg and left-side of the other leg (Fig. 1B). The vibrators were activated simultaneously, and the stimulation consisted of small amplitude vibrations (1.2 mm) of high (80 Hz) or low (40 Hz) frequencies. High frequency vibrations (80 Hz) applied to muscle tendons produce micro stretches of the muscle spindles which are interpreted by the CNS as resulting from a muscular stretch (Roll and Vedel, 1982; Roll et al., 1989; Gurfinkel et al., 1996). In free standing subjects, the vibration of hip abductor muscles acting in the frontal plane evokes spatially oriented postural responses (PR) with a latency of ~650 ms (Popov et al., 1999) which is aimed at correcting for perceived changes with respect to the vertical posture. The 40 Hz vibration frequency (hereinafter called Mecha Vib condition) favors activation of cutaneous afferents, essentially the Meissner corpuscles (Mountcastle, 1984). In the low frequency range (20–40 Hz), tactile stimulation of the sole of the foot gives rise to more powerful postural effects than those elicited by proprioceptive stimulation; conversely, this tendency is reversed with stimulation at higher frequencies. As the 40 Hz vibration would allow effects of the mechanoreceptive afferents to be separated from effects of proprioceptive signals (80 Hz), any confounding effect of mechanical cues with proprioceptive inputs are a priori excluded.

Seven subjects aged 24–29 years (mean age 25 years) without any known neurological and motor disorders, participated in the experiment. None of the participants was familiar with the purpose of the experiment. They all gave their informed written consent prior to undertaking the experiment, which was approved by the Ile de France ethic committee.

The experimental sessions consisted of 70 trials and started after verifying that the vibration induced lateral body tilt when the subjects stood still with the eyes closed. Subjects stepped over the obstacle in four conditions which were presented in a pseudo-randomized manner (no more than three trials of the same condition were presented consecutively). In 30% of these trials, no vibration was delivered (No Vib). In the remaining 70% of the trials, a 1 s-vibration was applied at low or high frequencies 400 ms before the fifth beep (i.e. on average −488 ms±150 before the APAs onset defined by the onset of the lateral force: Vib before) or at high frequency when the lateral force exceeded 2 N (on average +61 ms±128 after the APAs onset: Vib during).

The 80 Hz vibrations that occurred before the APAs onset were deliberately not early enough to evoke a PR. Here, the vibrations were used to induce afferent proprioceptive inflow analogous to the pattern resulting from body tilt in the opposite side to the vibrated muscles. This information, which arises from the Ia afferent inputs, could be seen as being conflicting with the forth-