Neuroscience 254 (2013) 285–300

MOVEMENT STRATEGIES AND SENSORY REWEIGHTING IN TANDEM STANCE: DIFFERENCES BETWEEN TRAINED TIGHTROPE WALKERS AND UNTRAINED SUBJECTS

F. HONEGGER, [a,b] **R. J. M. TIELKENS** [a] **AND J. H. J. ALLUM** [a*]

[a] *Department of ORL, University Hospital, Basel, Switzerland*

[b] *Biomaterials Science Center (BMC), University of Basel, Switzerland*

Abstract—Does skill with a difficult task, such as tightrope walking, lead to improved balance through altered movement strategies or through altered weighting of sensory inputs? We approached this question by comparing tandem stance (TS) data between seven tightrope walkers and 12 untrained control subjects collected under different sensory conditions. All subjects performed four TS tasks with eyes open or closed, on a normal firm or foam surface (EON, ECN, EOF, ECF); tightrope walkers were also tested on a tightrope (EOR). Head, upper trunk and pelvis angular velocities were measured with gyroscopes in pitch and roll. Power spectral densities (PSDs) ratios, and transfer function gains (TFG) between these body segments were calculated. Center of mass (CoM) excursions and its virtual time to contact a virtual base of support boundary (VTVBS) were also estimated. Gain nonlinearities, in the form of decreased trunk to head and trunk to pelvis PSD ratios and TFGs, were present with increasing sensory task difficulty for both groups. PSD ratios and TFGs were less in trained subjects, though, in absolute terms, trained subjects moved their head, trunk, pelvis and CoM faster than controls, and had decreased VTVBS. Head roll amplitudes were unchanged with task or training, except above 3 Hz. CoM amplitude deviations were not less for trained subjects. For the trained subjects, EOR measures were similar to those of ECF. Training standing on a tightrope induces a velocity modification of the same TS movement strategy used by untrained controls. More time is spent exploring the limits of the base of support with an increased use of fast trunk movements to control balance. Our evidence indicates an increased reliance on neck and pelvis proprioceptive inputs. The similarity of TS on foam to that on the tightrope suggests that the foam tasks are useful for effective training of tightrope walking. © 2013 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: tandem stance, vestibular, proprioception, sensory reweighting, movement strategies, center of mass (CoM).

INTRODUCTION

Human upright posture is more unstable during tandem stance (TS) than during feet side by side stance (Davis et al., 2010). Tightrope walkers, who are constantly training balance during TS on the rope, may control lateral sway of TS on the ground better than untrained controls. When adapting to the unstable postural conditions of the tightrope, a different movement strategy could be developed. This strategy could also be used in TS on the ground too and be different compared to the strategy of untrained subjects on the ground. Alternatively, roll sensory inputs could be weighted differently with tightrope training than weightings used by untrained subjects.

TS movement strategies

Most emphasis on the control of sway for two-legged stance with the feet side by side has been in the anterior–posterior (AP) direction. Several movement strategies have been used to describe AP sway for this posture. The simplified single segment inverted pendulum – introduced for the interpretation of stabilograms (Gurfinkel, 1973) – involves movements around the ankle joint, with lower-leg proprioception providing the main contribution to the postural control (Horak and Nashner, 1986; Fitzpatrick et al., 1992a,b; Fitzpatrick and McCloskey, 1994). Proprioceptive inputs arising from around the knee, hip, and lumbosacral joints were initially thought to have little or no influence on balance control (Nashner et al., 1982). In their pioneering paper Koozekanani et al. (1983) suggested, however, that upright stance is controlled in pitch by multi-segmental movement strategies. Further experimental and theoretical studies supported the multi-segment view and extended this concept to lateral sway (Day et al., 1993; Kuo, 1995; Hsu et al., 2007; Pinter et al., 2008). In fact, in-phase and anti-phase movements between the lower (legs) and upper body (trunk) have been shown to co-exist simultaneously in the pitch plane, representing low and high frequency modes of body sway, respectively (Bardy et al., 2002; Creath et al., 2005; Horlings et al., 2009b). Roll motion was shown to consist, as with pitch, of two similar movement strategies, one with trunk and pelvis moving in phase together, and the other with high frequency trunk movements about a relatively stable

---

[*] Corresponding author. Address: University Hospital Basel, Department of ORL, Petersgraben 4, CH-4031 Basel, Switzerland. Tel: +41-61-265-2041; fax: +41-61-265-2750.
E-mail address: John.Allum@unibas.ch (J. H. J. Allum).
Abbreviations: ANOVA, analysis of variance; AP, anterior–posterior; CNS, central nervous system; CoM, center of mass; CoP, center of foot pressure; GLM, generalized linear model; ML, medial–lateral; PSDs, power spectral densities; TFG, transfer function gains; TS, tandem stance; VBS, virtual boundary of stability; VTVBS, virtual time to virtual boundary of stability.

0306-4522/13 $36.00 © 2013 IBRO. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.neuroscience.2013.09.041

pelvis (Horlings et al., 2009b). Thus the question arises if the same two types of movement strategies are used in TS where roll motion is more unstable than in the feet side-by-side position.

Although TS is regularly used for clinical balance assessment and scientific studies about balance performance (Nichols et al., 1995; Smithson et al., 1998; Lamoth et al., 2009; Seino et al., 2009), little is known about the movement control strategies during TS. Winter et al. (1993) suggested that for normal, side-by-side, two-legged stance the mechanisms maintaining AP and medial–lateral (ML) stability consisted of independent ankle and hip strategies, with the ML direction dominated by a hip strategy, and the AP direction by an ankle strategy. For TS, Winter et al. (1996) postulated that postural control was achieved with an ankle strategy for ML sway, with little contribution from a hip strategy. In contrast the AP sway was dominated by a hip strategy with little contribution from the ankle strategy. However, several authors (Loram and Lakie, 2002; Morasso and Sanguineti, 2002) have questioned the assumptions used by Winter et al. (1996).

For TS on a tightrope it is inherently clear that lateral movements of the rope provide only a limited constraint on support surface movement and balance must be maintained by other means than torques generated at the foot (Otten, 1999). The minimal model abstraction that fits balance control requirements is a two segment inverted pendulum where upper trunk motion is used to generate torques rotating the swaying body back to upright (Paoletti and Mahadevan, 2012). Similarly for TS on a foam support surface, lower-leg somatosensory inputs are less reliable and the possibility of using these inputs efficiently to generate lateral torque is strongly degraded. For this reason one would expect a comparable movement strategy for this condition as standing on a tightrope. In summary, TS on foam might require a similar movement strategy as on a tightrope. If so, stance on foam would prove to be a safer means to compare tightrope walkers with controls.

In contrast to normal stance, the base of support in TS is enlarged in the AP direction compared to stance with the feet side-by-side resulting in an enhanced AP stability. In principle, the torque generated by pitching forward or backward during TS can be used to temporarily stabilize roll movements via a coriolis gyroscopic effect.

Training effects of TS

Lamoth et al. (2009) investigated if the level of athletic skill is reflected in a better control of body sway. Their subjects stood in TS on a narrow plywood strip. They found that skilful gymnasts had decreased trunk acceleration variability, indicating a more efficient postural control. They found that differences in skill did not depend on sensory reweighting, and suggested instead that expert gymnasts exhibited differences in the underlying postural control strategies which appear to be independent of the specific weighting of sensory information.

Sensory reweighting

Information about deviations from the upright position is accessible to the human brain through several sensory systems located on different body segments. The central nervous system (CNS) integrates these vestibular, visual, and somatosensory inputs into motor commands in order to maintain balance (Mergner et al., 2002; Peterka, 2002; Ravaioli et al., 2005; Goodworth and Peterka, 2009; Seemungal et al., 2009; Barra et al., 2010; Doumas and Krampe, 2010; Goodworth and Peterka, 2012; Sozzi et al., 2012). Depending on the balance task, the proportion of these sensory inputs may vary across body segments and with respect to center of mass (CoM) motion (Black et al., 1983; Allum and Honegger, 1998; Peterka and Loughlin, 2004; Creath et al., 2005; Cenciarini and Peterka, 2006; Allum et al., 2008; Fetsch et al., 2009; Goodworth and Peterka, 2010; Tjernstrom et al., 2010; Goodworth and Peterka, 2012; Billot et al., 2013). For tightrope walkers, it is an open question whether they use different weightings of sensory inputs to take full advantage of sensory dynamic ranges for the task of tightrope stance and whether they apply these weightings to TS balance tasks on a normal surface.

Sway during stance can be investigated by examining changes in the weighting between segment motion and by implication the composition of sensory feedback used to generate joint torques (Peterka, 2002; Maurer et al., 2006; Goodworth and Peterka, 2009). These authors applied small, 1 to 4 degrees of continuous support-surface perturbations to stance. They used the resulting amplitudes of CoM or trunk responses to argue, with the support of modeling techniques, that amplitude response nonlinearities (less relative sway with increasing stimulus amplitudes) demonstrated sensory reweighting. This modeling indicated a shifting reliance on ankle proprioception in favor of vestibular signals with increasing stimulus amplitude (Goodworth and Peterka, 2009; van der Kooij and Peterka, 2011). When roll motion was examined, it appeared that sensory weighting was less important for the upper body than for the lower body (Goodworth and Peterka, 2012). Thus in the context of different stance conditions, (Honegger et al., 2012a,b) for easier tasks, such as standing on a firm support surface eyes open, with little pitch or roll motion of the trunk with respect to the pelvis, lumbosacral and neck proprioceptive gains can be set high. However, when trunk motion is larger; for example when standing on a foam surface, eyes closed, vestibular gains would be set higher.

Head movements

Only a few studies have recorded head movements during normal unperturbed two-legged stance (Honegger et al., 2012a,b) and to our knowledge none during TS. Head movements are of interest because the