RESEARCH ARTICLE

A cutaneous positioning system

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Abstract Our previous work revealed that torso cutaneous information contributes to the internal representation of the torso and plays a role in postural control. Hence, the aims of this study were to assess whether posture could be manipulated by patterns of vibrotactile stimulation and to determine whether resulting modified postures were associated with specific and consistent spatial attitudes. Ten healthy young adults stood in normal and Romberg stances with six vibrating actuators positioned on the torso in contact with the skin over the anatomical locations corresponding to left and right external oblique, internal oblique and erector spinae muscles at the L4/L5 vertebrae level. A 250-Hz tactile vibration was applied for 5 s either at a single location or consecutively at each location in clockwise or counterclockwise sequences. Kinematic analysis of the body segments indicated that postural responses observed in response to single and sequential stimulation patterns were similar, while the center of pressure remained unaltered in any situations. Moreover, torso inclinations followed rectilinear-like path segments chartered by stimuli loci during sequential stimulations. Comparison of torso attitudes with previous results obtained with co-vibration patterns of the same duration showed that torso inclination amplitudes are equivalent for single (one location) and co-vibration (pairs of locations) patterns inducing the same directional effect. Hence, torso cutaneous information exhibits kinesthetic properties, appears to provide a map of upper body spatial configuration, and could assume the role of an internal positioning system for the upper body.

Keywords Proprioceptive positioning · Postural reorganization · Feedforward synergies · Cutaneous vibration

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Introduction

In the absence of visual information, our body representation in space and kinesthesia is primarily attributed to muscle proprioceptive information (Roll et al. 1989b; Kavounoudias et al. 1999a; Proske and Gandevia 2012), while a complementary/supplementary (Blanchard et al. 2011; Proske and Gandevia 2012; Blanchard et al. 2013) or substitutionary (Aimonetti et al. 2012) role is attributed to skin receptors. Major arguments supporting this assertion are based on the clear congruence between kinesthetic sensations and muscle spindle messages (Roll and Vedel 1982; Roll et al. 1989a) and persistence of kinesthesia following injuries affecting cutaneous pathways (Wall and Noordenbos 1977) or cutaneous anesthesia (Gandevia et al. 1983). However, cutaneous information from skin areas around limb distal joints has a significant proprioceptive role (Gandevia et al. 1992;

Edin 2001; Collins et al. 2005; Aimonetti et al. 2012) with vectorial properties (Aimonetti et al. 2007). Furthermore, a parallelism of encoding properties between muscle and type II cutaneous afferents was also shown for two-dimensional movements of the wrist (Aimonetti et al. 2012).

We recently showed that localized alterations of cutaneous information from torso areas by high-frequency vibrotactile stimulation (i.e., 250 Hz) result in small directional displacements of the torso and coordinated reorganization of the standing posture (Lee et al. 2012, 2013a, b). Torso inclinations were in the direction (azimuth) of the individually applied stimuli when stimuli were applied to anatomical locations corresponding to the internal obliques and erector spinae muscles location, and were congruent with a postural response to skin stretch. No displacement was observed for stimulations applied over the external oblique locations or simultaneous stimulation at all locations. In Lee et al. (2013a), we demonstrated that these postural responses consisted of coordinated reorganizations of posture by simultaneous multi-segmental reconfiguration of the body scheme with a concomitant invariance in the center of posture (COP). We also showed a summation effect of co-vibration (simultaneous vibration of two skin areas). These postural responses, stemming most exclusively from the cutaneous system (Lee et al. 2012, 2013a, b), are similar in nature (compensatory) to those resulting from muscle (e.g., Lackner and Levine 1979; Kavounoudias et al. 2001; Roll et al. 2009) or foot sole (Kavounoudias et al. 1999b; Roll et al. 2002) vibration, and are not associated with cutaneous reflexes (Lee et al. 2012) or startle responses. The uncovering of these properties leads us to suggest a proprioceptive role for torso cutaneous information. Hence, cutaneous proprioception is likely to contribute to the elaboration of the body spatial representation. For this study, we formulated the hypotheses that for the cutaneous system overlaying the torso prime mover muscles, directional encoding should present summation properties consistent with its associated function and tactile information may be used to "navigate" the map representing the spatial upper body scheme (represents a specific location on the internal body map). In other words, the cutaneous system may supply the feedback for a simple positioning system. To test these new hypotheses, we compared the vectors corresponding to torso inclinations induced by single and co-vibrations and analyzed postural reorganizations induced by the application of successive stimulations around the torso in clockwise or counterclockwise directions.

Materials and methods

Participants

Ten healthy young adults (five males, five females, mean age 22.0 ± 3.1 years), naïve to the purpose of the study,

with no neurological or functionally significant musculoskeletal dysfunction or a body mass index >30 kg/m^2 were recruited from a university student population. Each participant provided prior informed consent. The study was approved by the University of Michigan Institutional Review Board.

Instrumentation

Body segment kinematics were recorded by a passive motion capture system (Vicon MX, USA) from markers placed on commonly used landmark locations on each body segment or joint from the head to the ankle. Displacements of the center of pressure (COP) were recorded by a force platform (ORG6, AMT Inc., USA). All signals were sampled simultaneously at a frequency of 100 Hz. Vibrotactile stimulations were generated by six tactors (C2, Engineering Acoustics Inc., USA) placed on the skin over the areas corresponding to left and right internal oblique, external oblique, and erector spinae muscles at approximately the level of the L4/L5 vertebrae (anatomical references indicate location but do not imply an association with muscle stimulation). To manipulate posture without altering muscle proprioception, as justified previously (Lee et al. 2013a), we simulated localized skin stretch with a high-frequency sinusoidal vibration of 250 Hz and 200 μm peak-to-peak amplitude.

Procedure

Participants were instructed to maintain a relaxed upright standing posture [normal (feet hip-width apart) or Romberg (feet together) stance] while keeping their eyes closed and their arms at sides. Earplugs and earmuffs worn by all participants minimized audible cues possibly generated by the tactors and environment. The effects of three vibrotactile stimulation patterns, each including several conditions, were compared. The first pattern consisted of stimulations over single locations (termed single vibration; one black dot in Fig. 1); the second pattern consisted of simultaneous stimulations at two different locations (termed co-vibration; two black dots in Fig. 1) (e.g., Lee et al. 2013a). The third pattern involved a sequential application of stimulation (termed sequential vibration) at each location in a clockwise or counterclockwise fashion (Fig. 2a). For each pattern, the order of stance conditions (when stance was varied) and stimulation conditions was randomized.

For the single vibration pattern, participants completed 24 trials (6 single vibrations × 2 stances × 2 repetitions). For the co-vibration pattern, participants completed 20 trials (5 co-vibrations × 2 stances × 2 repetitions). Trials corresponding to single and co-vibration patterns included three 5 s consecutive periods consisting of pre-, per-,
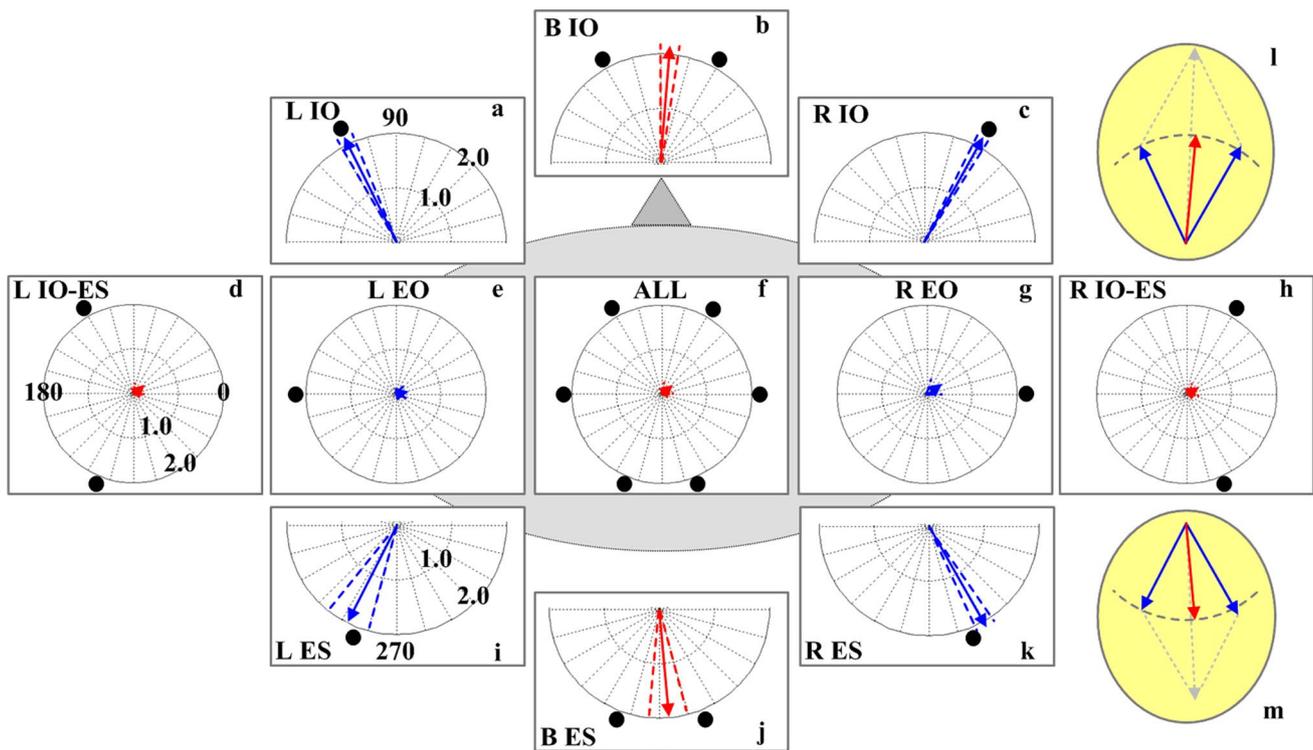
Fig. 1 Average postural shift vectors for single and co-vibration patterns. *Upper case labels* and *black dots* indicate the stimulation locations, as defined in text, for single (*blue*) and co-vibration (*red*) patterns. *Dashed lines* correspond to ±1 SD. Summation effects are illustrated in **l** and **m**, which combine **a**, **c**, **b** and **i**, **k**, **j** results, respectively. The constructed vector sums (*light gray*) show the directional summation, while the arcs underline the similar magnitudes for single and co-vibration patterns. [*IO* internal oblique, *ES* erector spinae, *L* Left side, *R* right side, *B* both locations, *ALL* all locations]

and post-vibration. For the co-vibration pattern, simultaneous stimulations were applied to the skin over the following locations: right and left internal oblique (B IO), right and left erector spinae (B ES), right IO and right ES (R IO-ES), and left IO and left ES (L IO-ES)—or all locations (ALL) simultaneously. For the sequential vibration pattern, eight trials (2 sequences × 2 stances × 2 repetitions) were performed. The sequential vibration patterns started at the RIO (Fig. 2a, ①) or LIO (Fig. 2a, ⑥) location for the clockwise and counterclockwise directions, respectively. Each sequence included eight 5 s consecutive periods consisting of no vibration (pre), six sequential vibrations (per), and no vibration (post).

Postural responses induced by vibration were quantified by body segment angles relative to the vertical, azimuth of torso inclination and COP displacements as a function of the tactile stimulation conditions (see one black dot or ⊗ in figures). Per-vibration responses were compared to data obtained in the pre- and post-vibration periods for each condition, between consecutive vibration periods within each condition and also between single and co-vibration pattern conditions obtained in previous experiments.

Data analysis

MATLAB (MathWorks, Natick, MA, USA) was used to process and analyze the signals recorded from the motion capture system and force plate. These signals were low-pass filtered with a zero phase, second-order Butterworth filter with a 10 Hz cutoff frequency, which is compatible with the spectral properties of the respective signals (Sienko et al. 2010; Verrel et al. 2011).

Changes in COP displacements and torso attitude were based on the displacement of the center of 95 % confidence interval elliptical fits to the respective trajectories for each period. The magnitude and direction (e.g., azimuth angle) of these displacements (ellipses center-to-center) were used to define the COP shift and postural shift vectors, as detailed in Lee et al. 2012. Changes in whole body posture were based on joint/body segment angles.

Analysis of variance (ANOVA) was used to test the main and interaction effects for each vibration pattern. Since trial repetition was not significant, the two repetitions of each trial were averaged for each participant for all dependent variables. Post hoc analysis for each dependent variable

Fig. 2 Average postural changes for the sequential patterns (*left panel* clockwise sequence, *right panel* counter-clockwise sequence). Stimuli locations (**a**), *top view* of torso mean inclination trajectories with *shaded areas* representing ±1 SD (**b**), three-dimensional trajectories of each marked joint (**c**), and COP trajectories (**d**). *Colors* and ⊗ correspond to stimuli locations
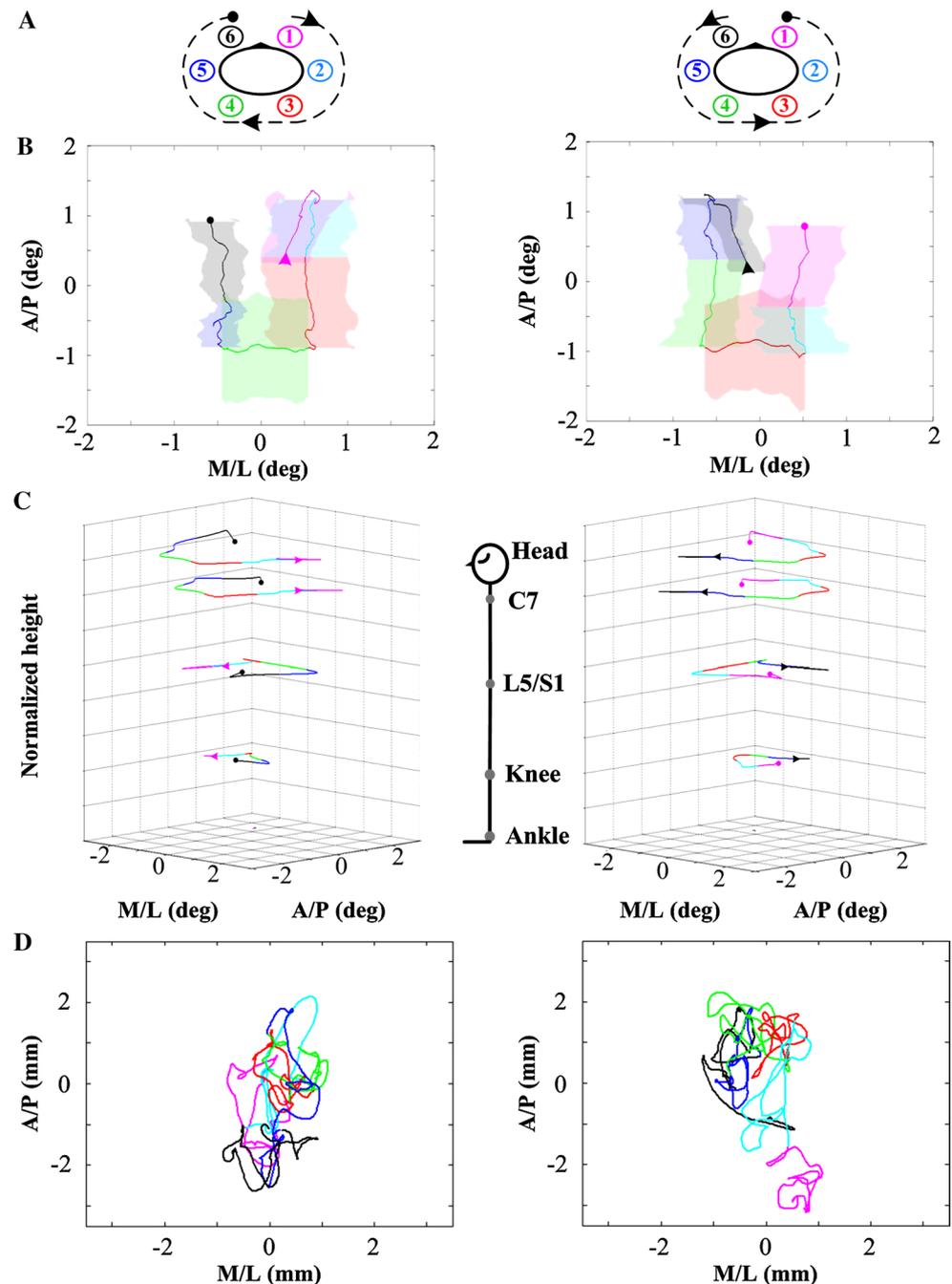
was performed using Sidak's method to determine which factors influenced the main and interaction effects.

Results

Stimulations using a single tactor induced significant directional torso inclinations (Fig. 1, blue vectors) consistent with previous results (Lee et al. 2012, 2013b). Co-vibration (Fig. 1, red vectors) of skin areas over the left and right internal oblique (Fig. 1b, B IO) and over the left and right

erector spinae muscle locations (Fig. 1j, B ES) induced significant ($P < 0.005$) forward and backward inclinations of the torso in the midsagittal plane, respectively, which correspond to the angular sums of the respective individual vectors (Fig. 1a + c, i + k). However, co-vibration over the left IO and ES (Fig. 1d) or right IO and ES (Fig. 1h) locations did not produce torso inclinations ($P > 0.30$), which also correspond to the angular summation of the individual directional effects and the absence of torso lateral flexion during skin vibration over the EOs locations (Fig. 1e, g). The lack of significant movement in the lateral directions

has been attributed to the greater stability of bipeds in the coronal plane (e.g., Martin et al. 1980; Winter et al. 1998). The absence of effect from simultaneous stimulation over all locations (Fig. 1f, ALL) is also in agreement with a summation of all individual effects.

The sequential application of stimulations in clockwise (Fig. 2, left panel) or counterclockwise (Fig. 2, right panel) directions produced sequential responses of significant magnitude ($P < 0.0001$) in specific directions ($P < 0.0001$), with a remarkable symmetry. In each case, postural changes (torso inclinations) traced rectilinear-like trajectories (Fig. 2b) whose end points were consistent with stimuli locations (Fig. 2a). While a single vibration in the coronal plane (EO) did not produce a significant effect when the initial posture was aligned with the gravito-inertial vector (Lee et al. 2012), the same stimulation applied during a sequential stimulation pattern (② or ⑤), which involved an initial posture not aligned with the gravito-inertial vector, produced a movement in the direction of the coronal plane. In addition, successive changes in torso inclination were concomitant to other joint displacements in space, which varied in magnitude and direction as a function of stimulation location (Fig. 2c). All joint displacements occurred in synchrony (no statistical lag differences ($P > 0.5$) between joint angle displacements), as observed for discrete co-vibration patterns (Lee et al. 2013a). Hence, successive stimulations induced successive postural reorganizations. However, neither the magnitude of the COP shift vector ($P > 0.40$) nor the elliptical fit to the area of the COP ($P > 0.43$) changed significantly during vibration compared to the pre-vibration period or between consecutive stimulations, regardless of the stimulation location. Average COP displacements are illustrated in Fig. 2d.

Finally, successive postural reorganizations induced by both sequential patterns ended in specific postural configurations quasi-identical to those induced by corresponding single stimulations, as illustrated in Fig. 3 (for visual rendering, joint angles are not scaled to stature). Indeed, the respective joint angle-defining postures were not significantly different ($P > 0.05$) between single and sequential vibration conditions.

Discussion

Summation of postural responses induced by concurrent vibratory stimulations intended to activate either proprioceptive receptors from different muscles or a combination of cutaneous and muscle receptors have previously been characterized by COP displacement (Ivanenko et al. 1999; Kavounoudias et al. 1999b). However, here we observed that symmetric homonymous (B IO or ES) and heteronymous (L or R IO-ES) stimulations resulted in "*directional*"

summations of the respective individual effects, but not in "*vectorial*" summations since the magnitude of torso inclinations induced by single and corresponding co-vibration conditions were nearly identical (Fig. 1l, m). This indicates that the sensory message elicited by a given vibration magnitude corresponds to a skin stretch magnitude, which is associated with a torso inclination of a specific magnitude. Therefore, quasi-identical vibrations applied to symmetric homonymous locations, such as B IO or B ES, elicit tactile information corresponding to similar torso inclination magnitudes, which does not produce an addition of individual responses, but rather a congruency. Therefore, our results and assumption are in complete agreement with the encoding properties of proprioceptive receptors contributing to position sense. This does not violate the principle of superposition since each set of stimulated receptors accomplishes the same function in terms of magnitude, and thus is not in contradiction with vectorial summations associated with magnitude differences between co-stimulations of different muscle groups (Kavounoudias et al. 1999b). The responses to both IO-ES co-stimulations result also from the same directional summation property. Indeed, displacement is insignificant since its resulting direction is equivalent to that of EO stimulation, which does not induce any postural change, as illustrated in Fig. 1e, g. Hence, such a summation demonstrates that skin stretch patterns encode torso spatial configurations (Fig. 3). Furthermore, since cutaneous information is de facto modified by muscle tendon vibration, then the corresponding postural responses and associated body representation (Lackner 1988; Roll et al. 1989b; Kavounoudias et al. 2001) inherently contain a tactile proprioceptive component. However, in this latter case, tactile and muscle spindle information mimic congruent stretches of the muscles and the skin, respectively; while in the case of selective tactile vibration the respective information is incongruent since muscle receptors are not stimulated (Lee et al. 2013a). Hence, we may argue that tactile information has precedence over muscle proprioception in postural control. Our assumption is in agreement with postural stabilization associated with simple finger skin contact with a fixed object when muscle proprioception is perturbed by vibration (Lackner et al. 2000; Slijper and Latash 2004).

The initial posture plays a critical role in the subsequent displacement of the torso, thereby revealing an important property of cutaneous information, as illustrated by the responses to simulation in the coronal plane (② or ⑤). Both sequential conditions showed that the final torso inclination achieved corresponded to the inclination elicited by the complementary single vibration condition. Indeed, when the torso moved into a new attitude (away from the coronal plane in the present case) in response to a preceding stimulation at a frontal or dorsal location (for example, ① or ④

Fig. 3 Final postures of each consecutive stimulation period in the sequential pattern conditions are very similar to those resulting from corresponding single stimulations. This occurred regardless of the pattern direction (clockwise or counterclockwise). The only difference between these conditions is the initial posture and thus the trajectory of body segment rearrangements. ⊗ corresponds to stimuli locations. Body segment angles are not scaled to size for visual rendering
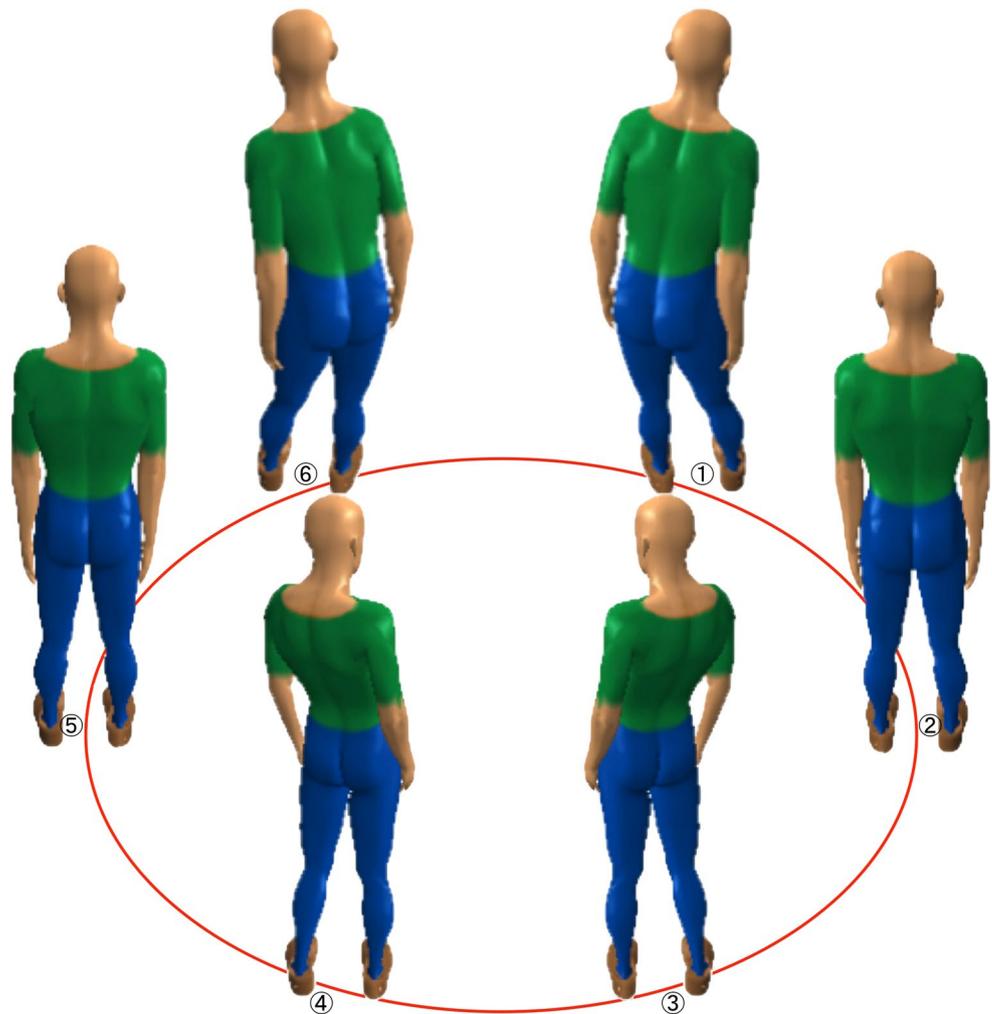
in clockwise condition), then the torso moved back to the coronal plane accompanied by a small tendency to reduce lateral flexion, as indicated by the inward direction of the trajectory (Fig. 2b). These results coupled with the rectilinear-like path traced by the torso, suggest that tactile manipulations can "move" the torso over a map in the transverse plane following the Cartesian coordinates associated with stimulation locations. Hence, the sensory system underlying the encoding of skin stretch could be considered as a cutaneous proprioceptive positioning system supporting the spatial representation of the torso. Although this role may also be attributed to muscle proprioception, calculation of torso inclination based on tactile information would likely be less computationally expensive for the central nervous system since complex inverse kinematic transformations (Katayama and Kawato 1993; Schweighofer et al. 1998) would be avoided.

However, the redundancy of the tactile and muscle proprioceptive systems may be used to optimize movement encoding by alternate substitution ("gating") of information from each proprioceptive modality as suggested by

Aimonetti et al. (2012) or to resolve representation uncertainties arising from incongruent information between sensory modalities. This parallels an assumption from Plato who argued: "our senses betray us"… "our judgment (about three fingers comparison example) cannot be one of the senses alone; the intellect must also be involved" (Plato 1966). Here, intellect may also be understood as the underlying process of sensory discrimination taking place in the cerebellum (Gao et al. 1996). This proposition may also be juxtaposed to the combination of muscle and tactile proprioceptive feedback (Blanchard et al. 2011). Since sensory incongruence was generated by modification of tactile information only, then the observed motor response in the direction of the stimulation indicates that (1) ambiguity was not resolved and (2) the movement is not compatible with a reduction of incongruence since it is compensatory for cutaneous information but not for muscle information. Therefore, the response indicates that cutaneous proprioception takes precedence over muscle proprioception in the present context. Then, it may be argued that, at least in the case of small movement amplitudes, information from

Fig. 4 (Color Online) Typical "primitive" synergies observed in a 13-month-old non-walking infant. These postural adjustments are produced systematically in response to the inclination of the supporting structure. Note flexion (*left*) and extension (*right*) of the arms concomitant to postural adjustments. All changes occur in syn-chrony as the basket is moved. The *yellow lines* underline torso and leg inclinations. These postural reorganizations are natural responses to changes in the center of gravity induced by the inclination of the supporting structure. Since the infant is holding the rim of the basket, these changes in posture are not necessary to maintain stability

only two sensory modalities is necessary but not sufficient to resolve incongruences or to suppress movement illusions. Overall, although compensatory responses triggered by the perturbation of one source of information show that the associated feedback is a component contributing to the control of an assigned motor function/goal, they also point out a weakness of the multisensory integration of proprioceptive information, which lacks robustness when facing incongruences/discrepancies. In addition, our perspective is in agreement with an improved proprioceptive acuity when both cutaneous and muscle proprioceptive information are available (Gandevia et al. 1983) and improved movement perception when tactile and proprioceptive stimulations are combined (Blanchard et al. 2011). Finally, incongruence between sensory modalities, as induced in our studies (Lee et al. 2012, 2013a, b) and others using vibration-modified proprioceptive information (e.g., Goodwin et al. 1972; Lackner and Levine 1979; Martin et al. 1980; Roll and Roll 1988), may be associated with cerebellar mechanisms processing sensory information (Gao et al. 1996). These mechanisms should be given more consideration when interpreting interferences between multi-modal proprioceptive information, beside possible spinal or supra-spinal interferences between pathways (Weerakkody et al. 2007).

Figure 2c illustrates the three-dimensional joint trajectories in response to sequential stimulations. The nominal changes in COP (Fig. 2d) are consistent with our previous results, which suggest that posture is reorganized to control the center of mass and thus COP displacement (Lee et al. 2012, 2013a). The resulting multi-segmental strategy in response to the successive modification of cutaneous information confirms that torso cutaneous information contributes to the internal spatial representation of the body and suggests a generalization of the contribution of cutaneous information to postural control and an inclusion of the cutaneous modality in the proprioceptive chain concept associated previously with muscle proprioception alone (Roll et al. 1989b; Kavounoudias et al. 1999b). Furthermore, the postural pantomime induced by sequential simulation appears to be the cutaneous correlate of muscle proprioception manipulations leading to two-dimensional movements (Roll et al. 2009).

Finally, changes in joint angles occur in synchrony without significant delay (Lee et al. 2013a). Hence, it is postulated that successive postural reorganizations are driven by the actuation of synergies to reduce the degrees of freedom to be controlled, in agreement with the concept proposed by Bernstein (Bernstein 1967), and thus avoid feedback delays that could compromise stability, in agreement with control theory (Jagacinski and Flach 2003). It is worth noting that these synergies appear very early in life (Forssberg and Nashner 1982), even before an infant can walk, as illustrated in Fig. 4.

To conclude, our results indicate proprioceptive properties of the cutaneous system are not confined to distal joints, despite inherent differences in distribution of receptors in the torso, and may play a more important role than previously admitted in vibration-induced movement alterations and thus motor control. In addition, the cutaneous modality appears to supply a "map" augmenting muscle kinesthesia. Hence, the skin may enclose a simple but extremely efficient proprioceptive system whose properties appear to parallel those of muscle proprioception. The cutaneous system may be comparable to an internal GPS. Finally, two major functions underlying postural responses to torso vibrotactile stimulation are accomplished simultaneously: adjusting posture as a function of sensory feedback changes and maintaining mechanical

stability of the bipedal system, while maintaining COP stability. The present results also intimate the importance of understanding the role of cutaneous information before using localized vibrotactile stimulations for sensory augmentation applications (Sienko et al. 2012); vibrotactile alarm signals intended to elicit volitional responses from the user may be incongruent or interfere with expected motor responses. In such cases, incompatibility and/or interference between a sensory message and its cognitively assigned association may reduce the efficacy of the assumed "augmented" feedback. Furthermore, repulsive cues used in torso-based vibrotactile feedback devices designed to stabilize posture are not compatible with natural messages; hence, this "assigned" association may not be optimal.

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