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Research report

Contribution of vision and cutaneous sensation to the control of centre of mass (COM) during gait termination

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Abstract

This study employed manipulation of sensory inputs (vision and plantar-surface cutaneous sensation) during gait termination to elicit insight into the roles played by these sensory systems in the control of gait termination. Attenuation of cutaneous sensation was achieved through hypothermic anesthesia. Visual information was occluded using special glasses. The subjects were asked to walk along an 8 m walkway and during randomly selected trials (25% of trials) to terminate their gait in a predetermined area. The centre of mass (COM) was obtained in order to provide an indication of the efficiency and stability during termination when sensory inputs were manipulated. Lack of visual information delayed the initiation of the slowing down of the COM forward progression and increased the step length of the last step of termination. Additionally, lack of vision resulted in the COM moving closer to the base of support (BOS) during double support and more variability, in the COM, when attempting to achieve a final stable position. Insensitivity of the plantar-surface mechanoreceptors led to a longer second step and a more variable foot placement of the first step, and increased the loading rate during the final two steps of termination. Additionally when vision and cutaneous information were absent the resolution of the final stable position was not as effectively controlled. The results demonstrated that visual information about self-motion and object-motion and sensation from the plantar surface of the foot play phase-specific roles in the control of COM during gait termination. © 2001 Elsevier Science B.V. All rights reserved.

Theme: Motor systems and sensorimotor integration

Topic: Control of posture and movement

Keywords: Cutaneous mechanoreceptor; Gait; Termination; Human; Foot

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1. Introduction

Sensation from the bottom of the feet has been demonstrated to play an important role during dynamic postural responses [1,11,12,14]. These dynamic postural responses include compensatory stepping in response to an unexpected platform perturbation [12,14] and feet-in-place responses due to either leaning [1] or galvanic stimulation [11]. From these studies the plantar-surface mechanoreceptors have been suggested to provide information about weight distribution, control during single support and the limits of the posterior base of support. Research has been done on the timing and magnitude of cutaneous afferent gating [5] and phase dependence of cutaneous reflexes [18] during walking. These studies have shown the importance of cutaneous afferent input in the control of locomotion. However, the role played by cutaneous afferent input in the feed-forward control of dynamic balance during gait has not been investigated. Gait termination is the transient state between cyclical gait and quiet standing. Thus gait termination provides a unique opportunity to study how the nervous system anticipates, controls and arrests forward momentum of the body. Therefore manipulation of sensory inputs during this activity may lead to changes in body centre of mass trajectory or foot placement that would give insight into the role played by that sensory system in the control of gait termination.

Descriptive studies of gait termination have illustrated

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the interplay between the centre of mass and centre of pressure during the termination phase [9]. The conclusions from this study were that during gait termination coarse control is achieved by foot placement and fine control during weight bearing is a result of the ankle musculature. Additionally, Jaeger and Vanitchatchavan [8] have detailed the profiles of the ground reaction forces that occur during gait termination. They found that two mechanisms appear to be used to stop forward progression during gait termination: an increased braking force in the first step after being signaled to terminate gait and a decreased push-off force in the trailing limb. Further to these findings Hase and Stein [6] found that if these two strategies were not effective, due to the COM moving outside the base of support, subjects would rise up on their toes to attempt to convert the forward motion of the COM into vertical motion to preserve a stable stopping position. The last resort, if all else fails, is to take another step.

The termination of gait is achieved through a progression of various mechanisms. The primary method of stopping is to reduce the push-off force from the stance limb, at the time of the signal to terminate gait, and increase the braking force exerted by first step after the signal to terminate gait. But how does the body obtain the information required to affect these changes quickly enough to stop gait and maintain a stable final posture? And if a stable position is not achieved what sensory information is used to initiate another step, if needed? One potential source is the sensation from the plantar surface of the foot. From previous work during compensatory stepping responses the cutaneous mechanoreceptors of the sole of the foot have been shown to provide information about the limits of the posterior base of support, control of single support and weight distribution during foot contact [12,14].

The other question posed in this investigation is what role does vision play in the termination of gait. Vision provides environmental information at a distance, information about self-motion and posture and movement of body segments relative to the environment [13]. Environmental information first and foremost provides cues to stop, such as an impending collision. Also this information is used to decide where to stop. These two types of information are uniquely specified by vision and cannot be easily substituted by other sensory modalities. Blind individuals can substitute both audio and tactile (through a cane) inputs to obtain some of this information, however it is not as accurate as the visual information. Information about self-motion and movements of body segments is useful for controlling the forward momentum, guiding foot placement and eventually maintaining final upright posture. It can be argued that vestibular and kinesthetic sensory systems can also provide this information. Although previous work during adaptive locomotion has shown this not to be entirely true [13]. For example when self motion information from vision is eliminated individuals are not able to maintain their position on the treadmill resulting in drift [13]. In this study we test this assumption by eliminating vision during the gait termination phase. Environmental cues to terminate gait were substituted by an audio signal and instructions tell the participants to stop in the next step thus specifying where to stop.

Therefore two important sources of information, cutaneous input from the feet and vision during gait termination were manipulated. Overall goal is to better understand the contribution of sensory input to the control of balance during gait.

2. Methods

2.1. Subjects

Six young healthy adult males (22–36 years; 171–188 cm; 65–95 kg) participated in this study. Prior to the experimental procedure each subject answered a medical screening questionnaire. This allowed for exclusion of subjects with problems affecting their balance or with conditions that would have been aggravated by the experimental protocol. The local research ethics board of the University of Waterloo approved the experimental protocol.

2.2. Methods

Attenuation of cutaneous sensation was achieved through hypothermic anesthesia. Subjects submersed the soles (lower 2–3 cm) of their feet in ice water for 15–20 min (this technique has been shown to be effective by Perry et al. [14]). Further to the initial cooling session the feet of the subject were submersed in ice water for 5 min after every block of 10 trials. This approach was adopted because the feet were becoming less affected by the cooling after a number of walking trials (maybe due to increase in peripheral circulation to warm the feet) vs. a standing situation that was evaluated during the previous studies using this same technique. To ensure that the sensation was adequately affected, cutaneous sensation measurements from the bottom of the feet were obtained using Von Frey filaments. The ‘method of limits’ was used to determine the sensory threshold from the centre of the heel pad (the exact position was along the midline of the foot and 20% of the foot’s length from the most posterior location on the sole of the foot). The subject was asked to respond with a verbal ‘‘yes’’ whenever they could feel the pressure on their foot (the subject was facing away from the experimenter during the testing and filaments were presented from high to low until one was detected and the next lowest was not). Each application of the filament was presented for less then a second and the filament was deformed to half its length so as to give a constant pressure (range 0.1–11 g). Fig. 4 illustrates that the Von Frey filament pressure required to elicit the perception of touch was twice as high during the cooling trials.

Visual information was occluded using special glasses (PLATO Model: P-1, Translucent Technologies Inc., Toronto, Canada), the glasses occluded vision when a 5 V signal was sent (at contact with the first force plate, the same time they would receive the signal to stop gait) to the glasses making the lens turn opaque. All other light was blocked from the top, sides and underside of the glasses so that when they were made opaque vision was completely blocked.

Two Optotrak (Northern Digital, Waterloo, Canada) camera banks were used to collect kinematic data. The sampling rate was 60 Hz and 22 infrared light-emitting diodes (IREDs) were employed to monitor the motion of the head, trunk and limbs. A 13 linked-segment model was employed to calculate the total body COM using the anthropometric data compiled by Winter [16]. The segments included in the COM determination were the head, chest, thorax, abdomen, pelvis, plus two upper and lower leg and arm segments. The motion of the following landmarks were recorded with IREDs placed anteriorly so they could be captured by the Optotrak cameras. The IRED's were positioned at the left and right ear canal, chin, left and right shoulders, left and right elbows, left and right wrists, xyphoid process, left and right first rib, left and right anterior superior iliac spine, left and right greater trochanters, left and right knees, left and right ankles and left and right fifth toes.

The trials were preformed along an 8-m walkway that has three force plates embedded in the floor (so that they were at the same level as the surface of the walkway). They were positioned so that termination occurred on the last two force plates (Fig. 1). During termination trials, a buzzer was used to signal the participants to terminate gait. Raw kinematic data and analog signals (from the force plates, glasses and trigger to the audio signal) were sampled for 10 s at 180 Hz.

2.3. Protocol

The subjects were asked to walk along an 8 m walkway and during randomly selected trials (25% of trials) to terminate their gait in a predetermined area. The walkway instrumented with three force plates was setup in the configuration depicted in Fig. 1. The stride length of the subject was measured so that we could position them so they would terminate on force plates two and three. Constant velocity was maintained via practice trials prior to the experiment (this was confirmed by measuring foot contact times (±5% within-subject variability) on the force plates). Gait termination took place with the feet of the subject stopping in a side-by-side placement at force plate numbered two and three in Fig. 1. At initial contact of force plate numbered one, the subject was randomly signaled (using an audible buzzer) to stop as soon as possible in the next step. Termination took place in 25% of the trials, 75% were walk-through trials. During half of the trials in each of the sensory conditions their vision was occluded using special glasses (PLATO Model: P-1, Translucent Technologies Inc., Toronto, Ontario) that turn opaque when a 5 V signal is sent to the glasses.

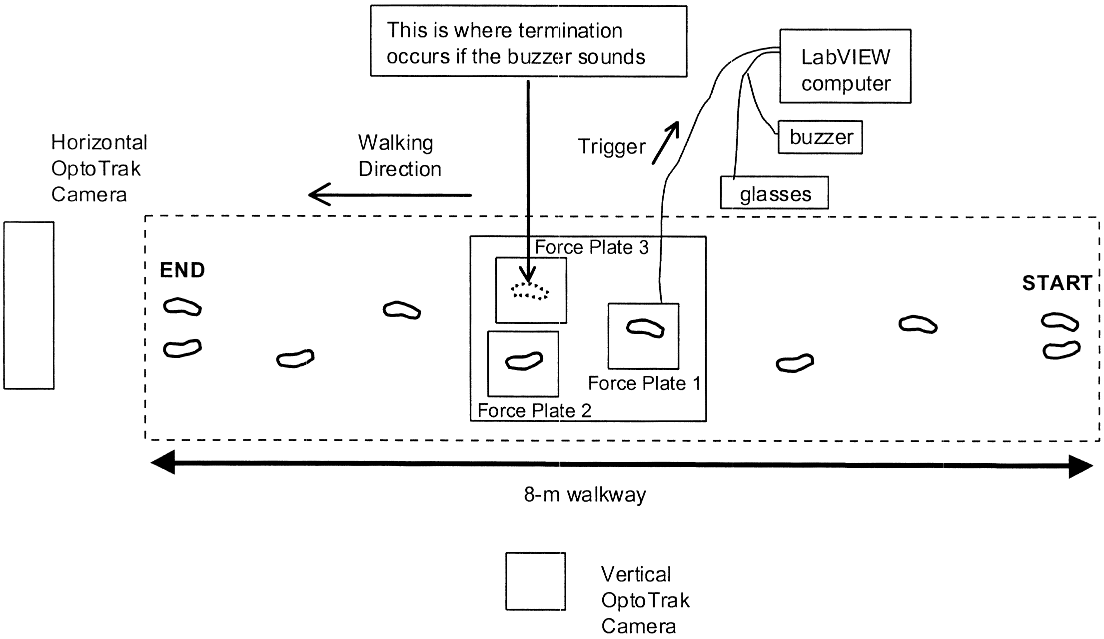

Fig. 1. Experimental setup. When the subject was signaled to terminate gait they would stop with the first (left) foot contacting force plate two and the second (right) foot contacting force plate three. Otherwise, in walk-through trials, the subject continued through until they stopped voluntarily.

2.4. Analysis

The centre of mass (COM) was obtained in order to provide an indication of the efficiency of termination and the stability during termination. Onset time of termination (T1) and time of termination (T2) completion were the first variables determined. T1 is the time at which the COM, during termination trials, deviated by more than two standard deviations from the average COM trajectory of the walk-through trials (T1 was measured relative to when the audio cue to terminate gait was given). T2 was determined by working backwards from a stable position at 3 s after T1 and then determining when the COM was no longer varying within two standard deviations of that stable position (see Fig. 2). The trial-to-trial variability of T1 and T2 were also recorded for each combination of sensation and visual condition. The root-mean-square of the COM in the anterior–posterior and medial–lateral directions during 1 s prior to time of termination (T2) was used as a indicator of stability at the completion of termination.

After determining the window of T1 and T2 the analyses continued with measures of step length and step width (during the first and second step of termination, Fig. 1). The variability of the step length and width measures was also calculated during each combination of sensation and visual condition during gait termination. Then the relationship of the COM to the base of support (BOS) was evaluated in the anterior–posterior and medial–lateral directions. Spatial COM distances from the front (COM–BOS$_F$), back (COM–BOS$_B$), right (COM–BOS$_R$) and left (COM–BOS$_L$) boundaries of the BOS were calculated (Fig. 3).

In order to determine the effects of sensation and vision on loading and unloading characteristics, the loading and unloading rates of foot contact were calculated from the vertical force recordings of the force plates. Loading rates were calculated for 100 ms after each foot contact. Additionally the unloading rate (for 100 ms prior to foot lift) was calculated during the step when the signal to terminate gait was given. Then the unloading rate of the first step of termination was calculated for 100 ms prior to the foot contact of the second step of termination.

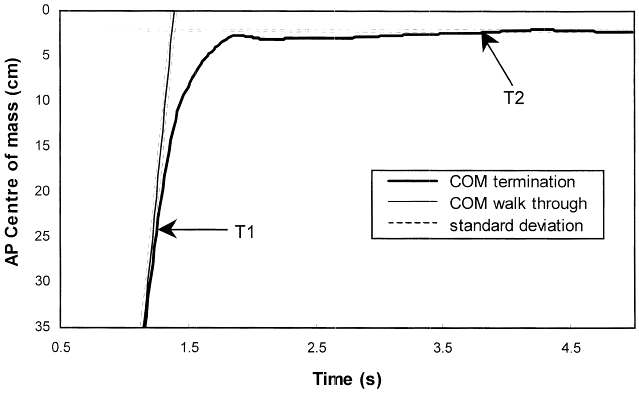

Fig. 2. Method to determine centre of mass deviation (T1) and time of termination (T2) variables. (AP=anterior–posterior).

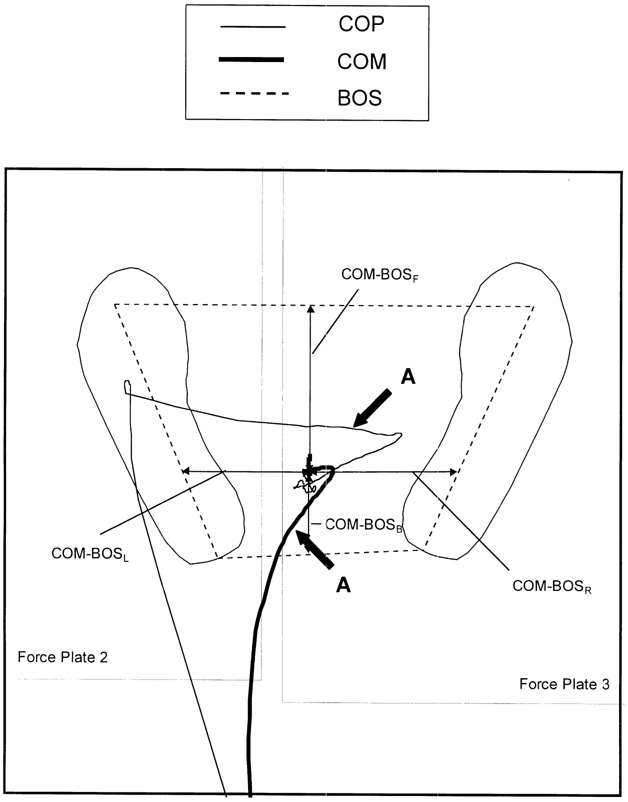

Fig. 3. Centre of mass (COM)–base of support (BOS) measurements taken during gait termination trials (F, forward; B, backward; R, right; and L, left). (A) Indicates time when both feet were flat on the ground.

Repeated measures ANOVAs were used to test for statistical significance in the measures mentioned above. The significance level was set at $P=0.05$. When appropriate the data was rank-transformed to ensure that the assumptions associated with the ANOVA were adhered to. The variability measures were log-transformed before the ANOVA was applied.

3. Results

Centre of mass (COM) in the termination trials deviated from the COM in the normal walk-through trials at an average of 0.86 s from the time when the signal to terminate gait was given. The time at which gait was terminated was on average 2.2 s after the time of the signal to terminate gait, thus making the average total time from initial COM deviation (T1) to gait termination (T2) was 1.34 s. The typical path of the COM in the horizontal plane was initially medial to the stance foot that struck force plate one, then moved towards the eventual first step of termination on the force plate two, thereafter the COM moves towards the second step of termination then comes to rest in the middle of the two feet (Fig. 3).

The time of COM deviation (T1) from the normal COM trajectory during walk-through trials occurred sooner during the cutaneous condition of reduced sensation, however not significantly (normal sensation (NS) 0.881±0.088 s vs. reduced sensation (RS) 0.841±0.093 s; $P=0.17$). The occlusion of vision significantly delayed T1 by 31 ms (full vision (FV) 0.846±0.087 s vs. no vision (NV) 0.877±0.096 s; $P=0.019$). The time of gait termination (T2) was unaffected by sensory condition (NS 2.23±0.35 s vs. RS 2.20±0.37 s; $P=0.45$) or visual condition (NS 2.21±0.37 s vs. RS 2.21±0.35 s; $P=0.93$).

The variability of the COM deviation (T1) and the time of gait termination (T2) were not significantly affected by the changes in sensory (T1: NS 72.8±49.3 ms vs. RS 83.6±40.3 ms; $P=0.47$; T2: NS 286.1±204.2 ms vs. RS 301.9±210.9 ms; $P=0.55$) or visual conditions (T1: FV 72.8±45.5 ms vs. NV 83.8±44.4 ms; $P=0.48$; T2: FV 299.6±221.7 ms vs. NV 288.4±192.1 ms; $P=0.68$).

The root-mean-square (RMS) of the COM in the medial–lateral direction was unaffected by sensory condition and visual condition independently. However, there was a significant interaction effect (combination of sensory condition and visual condition) on the RMS of the COM in the anterior–posterior direction ($P=0.01$). Further analysis revealed that the significant interaction effect was an increased RMS from the normal sensation/no vision (NSNV) to the reduced sensation/no vision (RSNV) condition (NSNV 0.018±0.013 cm vs. RSNV 0.026±0.016 cm; $P<0.05$).

The step width and step length of the first step were unaffected by sensory condition (step width: NS 17.5±3.1 cm vs. RS 18.0±3.3 cm; step length: NS 76.4±2.7 cm vs. RS 79.1±2.6 cm; P value's$>$0.18) and visual condition (step width: FV 17.8±3.2 cm vs. NV 17.7±3.3 cm; step length: FV 76.9±6.6 cm vs. NV 78.7±7.2 cm; P value's$>$ 0.22). The step width of the second step was also unaffected by sensory (NS 8.0±3.5 cm vs. RS 7.7±3.1 cm; $P=0.78$) and visual condition (FV 7.7±3.4 cm vs. NV 8.1±3.3 cm; $P=0.31$). In contrast the step length of the second step was significantly increased due to the sensory condition (NS 83.7±8.4 cm vs. RS 87.3±8.2 cm; $P=0.04$) and close to significantly increased due to the visual condition (FV 83.9±8.6 cm vs. NV 87.2±8.0 cm; $P=0.054$).

The variability of step width of the first step (NS 1.1±0.9 cm vs. RS 1.2±1.0 cm; $P=0.84$: FV 1.3±1.0 cm vs. NV 1.1±0.8 cm; $P=0.11$) and the variability of step width (NS 1.7±1.4 cm vs. RS 1.3±1.1 cm; $P=0.53$: FV 1.5±1.2 cm vs. NV 1.6±1.3 cm; $P=0.45$) and step length (NS 3.5±3.3 cm vs. RS 4.0±3.7 cm; $P=0.13$: FV 3.7±3.3 cm vs. NV 3.8±3.8 cm; $P=0.85$) of the second step were not significantly different between sensory or visual conditions. The variability of the first step length was increased (not statistically significantly) by a reduction in sensation (NS 1.6±1.3 cm vs. RS 2.8±3.4 cm; $P=0.055$), but unaffected by visual condition (FV 2.2±1.9 cm vs. NV 2.1±3.2 cm; $P=0.87$).

The proximity of the COM to the base of support, during the time between T1 and T2, was unaffected by either sensory condition or visual condition in three out of the four directions (forward (NS 3.8±1.6 cm vs. RS 4.1±1.7 cm; $P=0.47$: FV 4.0±1.7 cm NV 3.8±1.5 cm; $P=0.38$), backward (NS 17.9±1.8 cm vs. RS 18.1±2.0 cm; $P=0.73$: FV 17.9±1.9 cm NV 18.1±1.9 cm; $P=0.41$) and rightward (NS 13.1±3.9 cm vs. RS 13.2±3.2 cm; $P=0.80$: FV 12.9±3.7 cm NV 13.4±3.5 cm; $P=0.24$)). In the fourth direction, leftward proximity to the base of support, there was a strong trend towards a closer proximity of the COM to the BOS due to both change in sensory condition (NS 14.9±4.0 cm vs. RS 13.6±3.4 cm; $P=0.059$) and visual condition (FV 14.6±4.0 cm NV 13.9±3.6 cm; $P=0.065$).

The analysis of the loading on the force plates, indicated an increase in loading rate from normal sensation to reduced sensation, at both the first foot contact after being signaled to terminate gait (NS 9.48±2.26 kN/s vs. RS 10.31±2.38 kN/s; $P=0.042$) and the final foot contact of gait termination (NS 3.86±1.20 kN/s vs. RS 4.48±1.31 kN/s; $P=0.007$). There was no effect on the loading rate or unloading rate of the first contact prior to starting termination or the unloading rate of the force under the first step of termination prior to the contact of the final step of termination. Visual condition had no influence on loading/unloading characteristics.

4. Discussion

Investigation into the role of vision and cutaneous sensation (plantar-surface of the foot) in controlling the COM during gait termination required that the information from these two sensory sources be removed or reduced. The goggles provided complete occlusion of the participants' visual field. The effectiveness of the hypothermia to reduced sensation from the soles of the feet was demonstrated using Von Frey monofilament measurements taken throughout the experiment (see Fig. 4). Previous work (Perry et al. [14]) has also demonstrated that this method effectively reduces the sensation of the plantar-surface of the foot (measures of vibration, touch thresholds and two-point discrimination).

The overall goal of gait termination is to arrest the forward progression of the body to achieve a stable final upright posture. This is achieved in a specific sequence of events, first there is the initiation of termination at the time when the signal to terminate gait is given. In this segment of termination the central nervous system requires information about the present state of the forward progression of the body in order to initiate appropriate measures to terminate gait in the next two steps. Both input

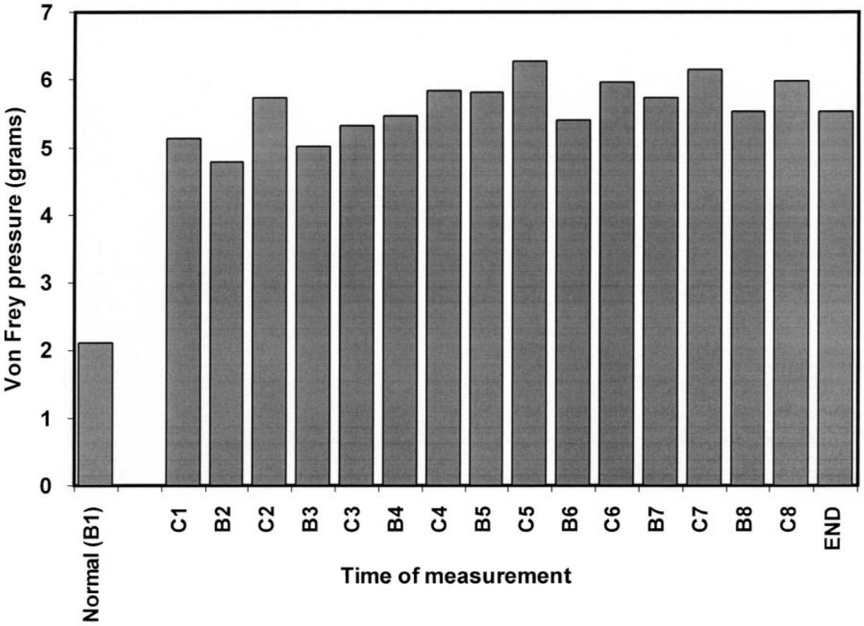

Fig. 4. Measurement of sensation from the plantar surface of the heel. This graph illustrates the increased amount of pressure (created by deflection of different diameters of the Von Frey monofilaments) needed to elicit a touch perception during hypothermia. (Normal (B1) is the measure taken before initial cooling, C=after cooling session #, B=before cooling session #).

from the plantar-surface mechanoreceptors and the visual system could provide information about the current state of the movement of the center of mass (COM). Plantar-surface mechanoreceptors could transduce the movement of the pressure under the foot as a result of the COM moving over top of it. Evidence for this role is demonstrated by the experiment of Kavounoudias et al. [10] who used vibratory stimuli under the soles of the feet that resulted in direction-specific body lean. The visual system could provide information about self-motion as transduced by stationary objects in the environment travelling across the retina thus giving an indication of the present COM movement. Only the manipulation of visual inputs delayed the initiation of termination (T1), therefore the visual system's perception of self-motion seems necessary in forming the initial response to begin to slow the COM when the signal to terminate gait is given.

The next segment of termination, after initiating the slowing of the forward progression in response to the signal to terminate, is the control during that same single support phase so that an appropriate foot placement can be achieved. The potential role of plantar-surface mechanoreceptors during this phase would be to provide information about the COM movement and the relationship between the centre of mass and the base of support (COM–BOS) in order to control the accuracy and location of foot placement. The lack of precision of control was demonstrated by the increase in variability of the first step length and the loss of control of location was indicated by the slight (non-significant) increase in step length during the reduced sensation trials. On-line feedback from the plantar-surface cutaneous mechanoreceptors about the movement of the COM could potentially play a role in the foot placement. The visual system also could provide information about foot placement through object-motion visual information of the swing limb and whole body motion, thus guiding foot placement for optimal position for control of forward progression. However, there was little support (a slight non-significant increase in step length) for this hypothesis involving vision's contribution to control during this phase. This is in contrast to obstacle avoidance studies where a clear effect of vision in control of limb elevation is seen [13].

Now within the first double support phase, this is when the main slowing-down of the COM is starting to occur [9], information about the COM movement is critical. Both plantar-surface mechanoreceptors and self-motion visual information have the potential to provide information for COM control. However, only plantar-surface mechanoreceptors seem to be playing a role during this phase as indicated by an increase in the loading rate, immediately following initial contact of the first step, during reduced sensation trials. The increase in loading rate indicates that the COM has not been effectively slowed prior to initial contact of the first step of termination. Post-hoc analysis of the COM velocity at the first step (NS 1.43 vs. RS 1.48 m/s; $P=0.049$) of termination revealed a higher velocity in the reduced sensation (RS) condition versus the normal sensation (NS) condition. The COM velocity was identical at initial contact when termination was triggered (NS 1.44 vs. RS 1.45 m/s; $P=0.68$). Additionally, it has been suggested that ankle kinematics during foot contact could effect the loading rate [2]. However, during this foot contact the ankle kinematics showed no difference (Ankle angle: NS 82.2° vs. RS 82.8°; $P=0.47$). The underlying mechanism for this could be the involvement of cutaneous information from the heel during foot contact in a short-latency reflex loop which initiates extension of the leg, rather than the usual withdrawal reflex, via reflex reversal [17,18] in order to slow the forward progression of the body's COM. Do and colleagues [3,4] have provided evidence, via their reduced plantar support surface experiments, that cutaneous information from the soles of the feet influences muscle activation patterns in both compensatory reactions and voluntary movements that could accomplish the slowing down of the COM.

During the transition from the first double support phase to the second single support phase, there is the requirement of information pertaining to the movement of the COM so as to maintain stability during one-legged stance and be able to accurately place the foot and achieve a final stable position. During this phase, information about the COM movement is potentially coming from both the plantar-surface mechanoreceptors and self-motion visual input and information about foot placement is coming from object-motion visual information and COM–BOS relationship from the plantar-surface mechanoreceptors. The increase in step length of the second step of termination as a result of the interaction of reduced sensation and no vision (marginally non-significant) conditions indicates that both information from plantar-surface mechanoreceptors and vision play important roles in foot placement, which is a key element in effectively controlling the COM movement [15]. The precision of control of the second step was unaffected as indicated by the absence of an effect of sensory or visual condition on the variability of foot placement.

The final phase of termination is a double support phase. This is when the COM is effectively controlled to a final stance position. There was further evidence that the plantar-surface mechanoreceptors are providing information to slowdown the COM progression (COM velocity: NS 0.53 vs. RS 0.55 m/s; $P=0.2$) in that there was an increased loading rate at initial contact of the second step of termination during reduced sensation trials. The ankle kinematics indicate that the opposite should be evident because the participants are landing more flat-footed in the normal condition (Ankle angle: NS 93.0° vs. 90.9°; $P=0.01$). The contradiction could be due to the small differences in ankle ankles (3° vs. 8°) when walking versus running. Other potential roles of both vision and plantar-surface mechanoreceptors during this phase is providing feedback information about the proximity of the COM to the BOS and also feedback information to control the amount of COM movement occurring during the final portion of termination when attempting to achieve a stable

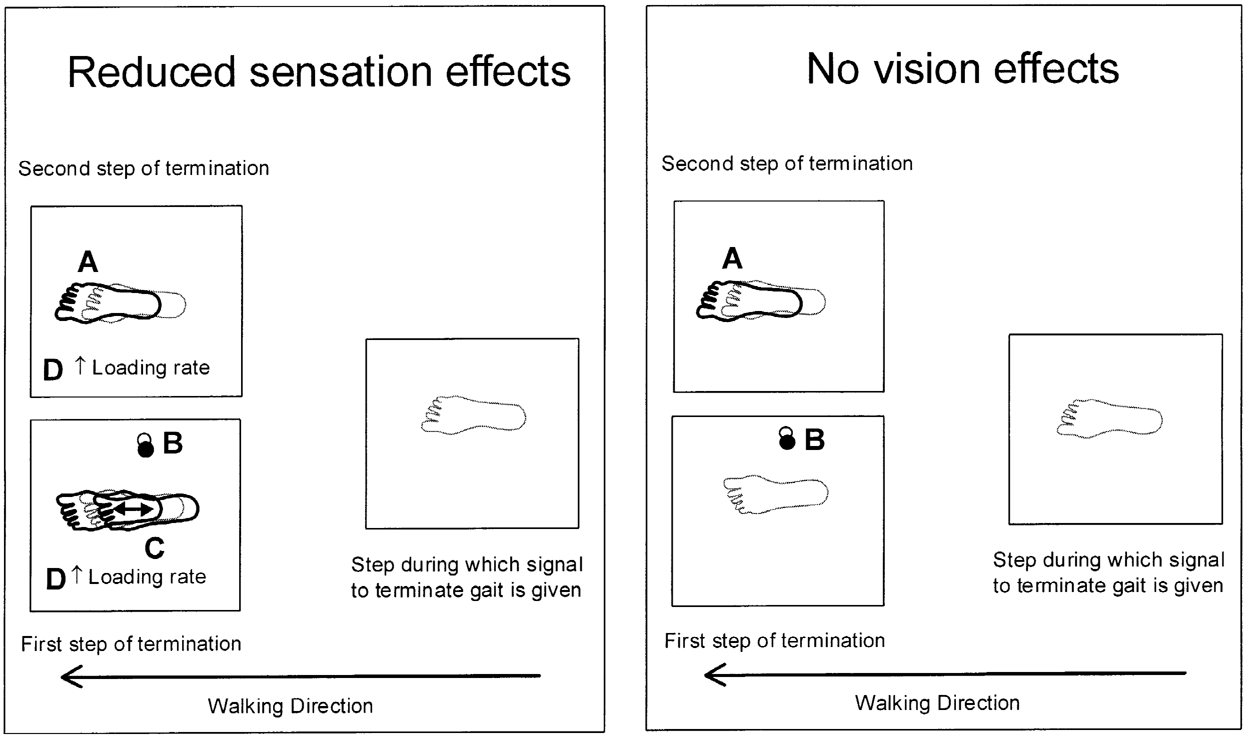

Fig. 5. Summary of effects of reduced sensation and deprivation of vision. (normal sensation or full vision foot placement is represented by the dashed/shaded footprints, the solid outline footprints indicate the effects); (A) an increase in step length of the second step; (B) a reduction in leftward proximity of the COM to the BOS; (C) an increase variability in step length; and (D) an increase in loading rate at foot contact. Lack of vision also delayed the onset of termination (T1). The resolution of the final COM position was dependent on the interaction of sensory condition and visual condition.

position. The first role was supported in both the reduced sensation and no vision conditions, in that the COM approached closer to the left perimeter of the BOS. This direction was most likely the only one affected because the COM is moving leftward as the last step of termination is occurring, so the control of the COM's proximity to the left side of the BOS is the only one that will require precise control during the final double support phase. The resolution of the final position in the anterior–posterior direction was increased by reduced sensation, however only in the no vision condition. This finding illustrates the role of plantar-surface mechanoreceptors role in the fine control of a final stable position only when vision is absent. This provides further evidence that multiple sensory systems are used for control of postural strategies [7].

In summary, visual information about self-motion and object-motion and sensation from the plantar surface of the foot play phase-specific roles in the control of COM during gait termination (Fig. 5). Visual information is involved in the initiation of slowing down the COM forward progression and in guiding foot placement to effectively corral the COM during single support. It is also used to detect COM motion relative to the BOS during double support and providing complementary information of COM movement for feedback in achieving a final stable position. Plantar-surface mechanoreceptors provide feedforward information about COM movement during single stance for accurate and precise location of foot placement, and provides feedback information about foot contact in order to initiate braking forces to slow down the forward progression of the COM. Additionally when vision is absent it is important in resolving a final stable position.

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References

[1] H. Asai, K. Fujiwara, H. Toyama, T. Yamashina, I. Nara, K. Tachino, The influence of foot soles cooling on standing postural control, in: T. Brandt, W. Paulus, W. Bles, M. Dieterich, S. Krafczyk, A. Straube (Eds.), Disorders of Posture and Gait, George Thieme-Verlag, New York, 1990, pp. 198–201.

[2] B. De Wit, D. De Clercq, P. Aerts, Biomechanical analysis of the stance phase during barefoot running and shod running, J. Biomech. 33 (2000) 269–278.

[3] M.C. Do, M. Gilles, Effects of reducing plantar support on anticipatory postural and intenetional activities associated with flexion of the lower limb, Neurosci. Lett. 148 (1992) 181–184.

[4] M.C. Do, A. Roby-Brami, The influence of a reduced plantar support surface area on the compensatory reactions to a forward fall, Exp. Brain Res. 84 (1991) 439–443.

[5] J. Duysens, A.A.M. Tax, S. Nawijn, W. Berger, T. Prokop, E. Altenmuller, Gating of sensation and evoked potentials following foot stimulation during human gait, Exp. Brain Res. 105 (1995) 423–431.

[6] K. Hase, R.B. Stein, Analysis of rapid stopping during human walking, J. Neurophysiol. 80 (1998) 255–261.

[7] F.B. Horak, L.M. Nashner, H.C. Diener, Postural strategies associated with somatosensory and vestibular loss, Exp. Brain Res. 82 (1990) 167–177.

[8] R.J. Jaeger, P. Vanitchatchavan, Ground reaction forces during termination of human gait, J. Biomech. 25 (1992) 1233–1236.

[9] Y. Jian, D.A. Winter, M.G. Ishac, L. Gilchrist, Trajectory of the body COG and COP during initiation and termination of gait, Gait Posture 1 (1993) 9–22.

[10] A. Kavounoudias, R. Roll, J.-P. Roll, The plantar sole is a 'dynamometric map' for human balance control, NeuroReport 9 (1998) 3247–3252.

[11] M. Magnusson, H. Enbom, R. Johansson, J. Wiklund, Significance of pressor input from the human feet in lateral postural control, Acta Otolaryngol. Stockholm 110 (1990) 321–327.

[12] B.E. Maki, S.D. Perry, R.G. Norrie, W.E. McIlroy, Mechanical facilitation of sensation from plantar foot-surface boundaries: effects on postural stabilization, J. Gerontol. 54A (1999) M281–M287.

[13] A.E. Patla, How is human gait controlled by vision?, Ecol. Psychol. 10 (1998) 287–302.

[14] S.D. Perry, W.E. McIlroy, B.E. Maki, The role of cutaneous mechanoreceptors in the control of compensatory stepping reactions evoked by unpredictable, multi-directional perturbation, Brain Res. 877 (2000) 401–406.

[15] D. Winter, A.B.C. (Anatony, Biomechanics and Control) of balance during standing and walking, Waterloo Biomechanics, Waterloo, Ontario, 1995.

[16] D.A. Winter, Biomechanics and Motor Control of Human Movement, 2nd Edition, Wiley, Toronto, 1990.

[17] J.F. Yang, R.B. Stein, Phase-dependent reflex reversal in human leg muscles during walking, J. Neurophysiol. 63 (1990) 1109–1117.

[18] E.P. Zehr, R.B. Stein, What functions do reflexes serve during human locomotion?, Prog. Neurobiol. 58 (1999) 185–205.