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RESEARCH ARTICLE

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Effects of head immobilization on the coordination and control of head and body reorientation and translation during steering

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Abstract Changing the direction of locomotion involves lateral translation of the body in addition to body reorientation to align with the new travel direction. We designed this study to investigate the CNS control of these postural adjustments. The specific aims of the study were: first, to test the hypothesis that anticipatory head movements towards the new travel path are proactively controlled by the CNS to provide a stable frame of reference for body reorientation and, second, to investigate the relative contribution of foot placement and other mechanisms to the control of lateral body translation during steering. We achieved these aims by carrying out a comprehensive biomechanical analysis of participants performing a steering paradigm and observing the effects of immobilizing the head (by fixing it to the trunk) on postural control and the sequencing of body segment reorientation. Participants performed a task whereby they were visually cued to change their direction of walking by 30° or 60°, left or right, at the midpoint of a 9-m path. The temporal sequence of body reorientation was consistent with previous findings that the head starts to turn in the direction of travel before the rest of the body. Translation of the centre of mass (COM) in the new travel direction was achieved both through alternate placement of the contralateral foot prior to the turn step and use of a hip strategy to control the body pendulum during swing. Immobilizing the head resulted in the following significant changes: earlier onset of trunk yaw with respect to cue delivery, later trunk roll onset and a reduction in trunk roll amplitude. These results provide valuable information regarding the biomechanics of steering and support the hypothesis that aligning the head with motor or locomotor goals using vision provides the CNS with a stable frame of reference, independent of gaze, that can be used to control the repositioning of the body in space.

Keywords Locomotion · Heading · Direction change

Introduction

Online steering to avoid obstacles or to reach specific goals in the environment is an integral component of adaptive locomotion and involves reorienting the body in space. This requires a dynamic updating of the relationship between the body and the environment. Three main sensory systems are involved in this process: vision, the vestibular system and proprioception. Ascending pathways conveying information from these systems connect with specific areas in the brain related to representation of space. Individual neurones which fire selectively when the head is pointed in a specific direction have been described in the thalamus and postsubiculum of rats (McNaughton et al. 1996). “Head direction cells” with similar properties have been described in the primate presubiculum (Robertson et al. 1999). Therefore reorienting the head in the new travel direction (identified by vision) can provide the CNS with an allocentric frame of reference that can be used to reorientate the rest of the body.

Pozzo et al. studied a wide variety of locomotor tasks and postulated that the neural control of head movement plays a key role in trunk/leg coordination (Pozzo et al. 1990, 1992, 1995). They described periods of stabilization of head in space, whilst the body was moving during locomotor tasks ranging from normal forward walking to backward somersaulting. This suggested that head placement and stabilization provides a stationary frame of reference (an “inertial guidance platform”) for the coordination of the many body segments.

Flanders et al. (1999) found that when stepping forward and reaching to touch remembered target locations

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("virtual target"), subjects made significantly larger errors in their final hand position than when reaching to visible targets. Subjects were found to rotate the head less in the virtual-target condition (resulting in a more limited range of head postures) and the final head angles (at the end of the movement) were geometrically related to the incorrect hand locations. These results support the authors' hypotheses that stabilization of the head in space provides a platform for body coordination during locomotion and that stabilization of the head and eyes on the target normally provides a gaze-centered frame of reference for the coordination of whole body reaching.

Grasso et al. (1996) found that human adults walking in circles consistently rotated their heads towards the inner concavity of the walking trajectory and that head direction systematically anticipated changes in the direction of locomotion (by around 200 ms). The authors subsequently investigated head and gaze orientation in subjects walking around a corner (i.e. changing direction by 90°) either with eyes open or closed (Grasso et al. 1998). They found that head and eyes systematically deviated towards the future direction of the curved trajectory with a lead of around 1 s. Strikingly, the same behaviour was observed in darkness (eyes closed). During backwards walking around the same corner (reverse of the forward trajectory) gaze deviated in the opposite direction, to align with the future plane of progression (albeit in the opposite direction). The authors propose a feedforward navigation control system governing synergic head and eye movements aimed at anticipating future motor events.

The results of these studies suggest that aligning the head with motor or locomotor goals using vision provides the CNS with a stable frame of reference with respect to the environment that can be used to control the repositioning of the body in space. However, hitherto no attempt has been made to determine to whether these anticipatory head movements are generated as part of the process of reorienting gaze with the new travel direction or whether head alignment provides a frame of reference that is independent. We addressed this issue in the present study by immobilizing participants' heads with respect to the trunk and observing changes in their ability to change walking direction. This experimental approach removes the possibility of independent head movement while still allowing independent gaze reorientation (using eye movements). Spatial or temporal changes to participants' steering characteristics under these conditions would provide supportive evidence for an independent role for proactive head alignment in the guidance of steering. In order to determine how steering characteristics are affected by head immobilization, we first need to know how body repositioning is normally achieved.

Mechanics of changing direction

Changing direction involves: (a) rotation of the body toward the new direction of travel and (b) lateral translation of the centre of mass. These changes are superimposed on the normal forward progression of the centre of mass.

Rotation

Rotation of the whole body towards the new line of travel is accomplished during the turn step mainly through the action of the stance limb (Patla et al. 1991). Because the foot is in contact with the ground and there is minimal rotation at the knee, the major rotary action has to come from the hip rotators.

Centre of mass translation

One method by which lateral centre of mass (COM) acceleration in the turn direction may be regulated is by controlling foot placement via hip abductor/adductor activity during the swing phase of the previous step. Increased hip abductor activity will increase step width, and decreased abductor (or increased adductor) activity will reduce step width (Winter 1995). Foot placement is the primary determinant of the position of the centre of pressure (COP) and the difference between the COP and COM dictates the centre of mass acceleration magnitude and direction during walking (Winter 1995).

Another way to regulate lateral COM acceleration is through control of the body pendulum through appropriate action of ankle inverters/everters and hip and trunk musculature during the turn step (McKinnon and Winter 1993; Winter 1995). This can be achieved by controlling the inverted pendulum in the frontal plane through the activity of the ankle inverters/everters. However, since these muscles are relatively weak and the inertia of the pendulum is large, this strategy is not very effective (Winter 1995).

A more effective way to move the body COM laterally is through muscle action at the hip and trunk. This kind of "hip strategy" was first described by Horak and Nashner (1986) in a study of participants' reactions to forward and backward platform perturbations. The authors showed that, in response to perturbations, each participant's body behaved like a double pendulum with rotation about the ankle and the hip joint. For example, when a large platform perturbation caused the body to fall backwards individuals rotated the legs backwards while rotating the upper body forwards (i.e. generating pitch movements about the hip joint), thereby causing the COM to move forward. Extending this to the frontal plane, *roll* movements about the hip joint will serve a similar function in controlling the COM acceleration in the M/L plane. It has been demonstrated that strategies used to recover from an unexpected perturbation have also been used to recover from a predictable perturbation. For example, Cordo and Nashner (1982) and Frank and Earl (1990) showed that similar balance recovery strategies (characterized by muscle sequencing) were

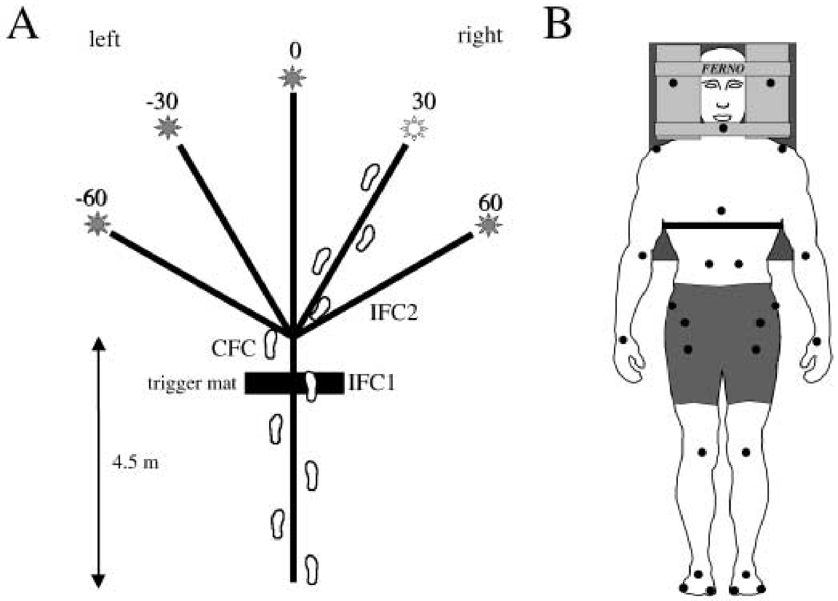

Fig. 1 **A** Schematic diagram of the steering paradigm. When the subject stepped on a trigger mat, placed towards the mid-point of the travel path, one of five cue lights (placed at floor level) lit up denoting the required walking direction. The footprints represent a typical foot placement profile for a 30° right turn trial [*IFC1* (ipsilateral foot contact 1) the start of the transition stride (concurrent with cue delivery), *CFC* placement of the contralateral foot (i.e. contralateral with respect to required turn direction), *IFC2* end of the transition stride]. **B** Anatomical placement of OPTOTRAK infrared markers and method of immobilizing the head with respect to the trunk. The FERNO head immobilizer was attached to a rigid board that was strapped around the subject's chest

used in response to a perturbation to the upper body whether it occurred because a handle the individuals were holding onto pulled or pushed them unexpectedly or the individuals themselves pushed or pulled on the handle. These results suggest that hip strategies can be used in a predictive manner to control COM behaviour. Recently, Patla et al. (1999) presented evidence that participants adopted a M/L hip strategy, observed as changes in trunk roll profiles, when changing the direction of locomotion. However, full body kinematic data were not measured in this study and therefore the relationship between postural changes and lateral COM behaviour was not investigated.

Aims

This study was designed to achieve two main objectives:

1. To test the following working hypothesis: *Anticipatory head movements towards the new travel path are proactively controlled by the central nervous system to provide an independent frame of reference for the lateral translation and reorientation of the rest of the body*. This was achieved by determining the sequence of head, trunk and leg reorientation during a steering paradigm and observing the effects of immobilizing the head with respect to the trunk on this sequencing. The prediction based on our hypothesis was that head rotation would normally precede that of the rest of the body and that preventing independent head movement would result in earlier trunk reorientation to compensate for the loss of independent head mobility.
2. To perform comprehensive biomechanical analyses in order to investigate the relative contribution of foot placement and other mechanisms to the control of COM translation during steering.

Materials and methods

Participants

Five healthy adults (four female, one male, age 24.8±2.6 years, height 170±7.3 cm, weight 61.3±3.8 kg) volunteered for the study. The experimental protocol was approved by the University of Waterloo Ethics Committee and all participants gave informed consent. Exclusion criteria included any self-reported neurological, musculoskeletal or visual impairment. Participants (n=5) were instrumented with 28 infrared diodes placed bilaterally on various anatomical landmarks (see Fig. 1): These active markers were tracked using the OPTOTRAK motion analysis system (Northern Digital Inc., Canada). Knowledge of their positions over time allowed calculation of various kinematic parameters. For 50% of trials the participant's head was fixed to the trunk using a modified Ferno Universal Head Immobilizer attached to a rigid board strapped to the participant's back.

Protocol

Participants walked at their natural self-selected pace along a 9-m straight travel path. At the mid-point of the travel path subjects were visually cued via lights placed on the floor at the end of each pathway (Fig. 1). Participants were required to either continue walking straight or to alter direction by either 30° or 60° to the left (counterclockwise) or to the right (clockwise). Light cues were activated when participants stepped on a pressure-sensitive mat placed one step length before the midpoint of the straight travel path such that the participant had one stride duration (two steps) to plan and implement a direction change. Participants were instructed to start walking with either their left or right leg depending on the required turn direction so that they were never required to cross one leg in front of the other in order to turn successfully. Subjects were only required to turn during 50% of trials. Five trials were collected for each of the four turn conditions (30° left, 60° left, 30° right and 60° right) along with ten trials for each straight path condition (starting walk with left leg and starting with right leg). All trials (40 total) were randomized. The same number of trials was collected in the head immobilized (HI) condition. Due to the long setup time required to fit the participant with the head immobilizer, HF and HI trials were separated. However, the presentation of HF or HI trial blocks was counterbalanced between subjects.

Data analysis

Various kinematic measures were obtained. Pitch, roll and yaw angular displacement profiles of the trunk and the head in the global reference frame were determined from the three non-co-linear markers placed on the trunk and the head. The three markers define the rigid body of the trunk and the head, making it possible to determine their orientation with respect to gravito-inertial frame. A 14-segment anthropometric model of COM was determined (including legs and feet, thighs, upper arms, forearms, head, pelvis and a four-segment trunk) allowing calculation of COM displacement in the M/L plane (Winter et al. 1997). Position of the ankle markers in 3D space was used to determine the step width and step length at each double support phase of the step cycle. The timings of foot contact and toe-off were also measured for each leg. Foot contact was measured as movement termination of the ankle marker in the A/P plane. Toe-off was measured as the onset of vertical movement of the toe markers.

The mean values of the above measures were calculated at three discrete times during the transition stride over which participants implemented the turn: onset of the transition stride [time of heel contact of the ipsilateral foot (with respect to turn direction) IFC1 and also time of cue delivery], contralateral foot contact (CFC) and termination of transition stride (IFC2) (see Fig. 1).

In order to determine the sequence of reorientation of various body parameters during a turn, data obtained from ten control trials, for each subject, condition and turn direction, were averaged over time relative to the instant of cue delivery. Standard deviation profiles over time were also generated. The onset of change in trunk and head yaw reorientation during a turn trial was measured as the point in time that test data deviated from the control average profile (providing the deviation continued beyond the control 2SD boundary). A similar strategy was adopted to determine the onset of change in mediolateral COM position and leading foot displacement in the direction of the new travel path.

A repeated measures ANOVA was performed on each measure. Depending on the measure the number of levels in the ANOVA varied; the levels are described in “Results”.

Results

Raw data

Figure 2 shows typical profiles of head yaw, trunk yaw, trunk roll, and ipsilateral foot and COM displacement in the M/L direction. For illustration purposes data obtained from individual trials were time-normalized with respect to the transition stride [first ipsilateral foot contact *(*IFC1 in Fig. 1) to the second ipsilateral foot contact (IFC2 in Fig. 1)]. Average profiles over five trials were generated for one individual for each experimental condition (straight, 30° and 60°, both left and right). The left panel shows averaged data obtained from the HF condition (head free) and the right panel averaged data obtained from the HI (head immobilized) condition.

During normal straight path locomotion, head and trunk yaw displacements were minimal, and the ipsilateral foot trajectory had minimal deviations in the mediolateral plane (see solid lines in Fig. 2). Trunk roll movements showed a cyclical pattern during normal straight path locomotion (less than ±3°): trunk deviated to the right during the right stance phase and to the left during the left stance phase. When participants were required to change direction to the right, as expected head and trunk rotated to the right (yaw angle deviations in the clockwise directions) to reorient the body in the direction of travel, and the right foot trajectory showed displacement to the right during the swing phase to control foot placement on the new travel path. The COM was also displaced to the right, which reflects lateral translation of the body in the direction of the turn. In addition trunk roll angle deviations to the left were observed. The reverse situation was observed when participants were required to change direction to the left. Because of the nature of the task, no significant changes in the sagittal plane were expected; therefore the pitch profiles are not included in Fig. 2. However, statistical analysis of all profiles (roll, pitch and yaw) of the head and trunk was performed. The following significant results were obtained.

Sequence of reorientation

There was a clear sequence of reorientation onset in the HF condition; first head yaw, then trunk yaw, trunk roll, COM, and finally ipsilateral foot M/L displacement. The mean values of onset latency with respect to cue delivery for each parameter are shown in Fig. 3. The dotted line shows the mean time of onset of the turn step (onset of swing immediately prior to IFC2). On average, onset of the turn step (toe-off) was earlier (by 170 ms) than onset of M/L foot displacement, i.e. the foot moves forward for a distance following toe-off before it is moved laterally.

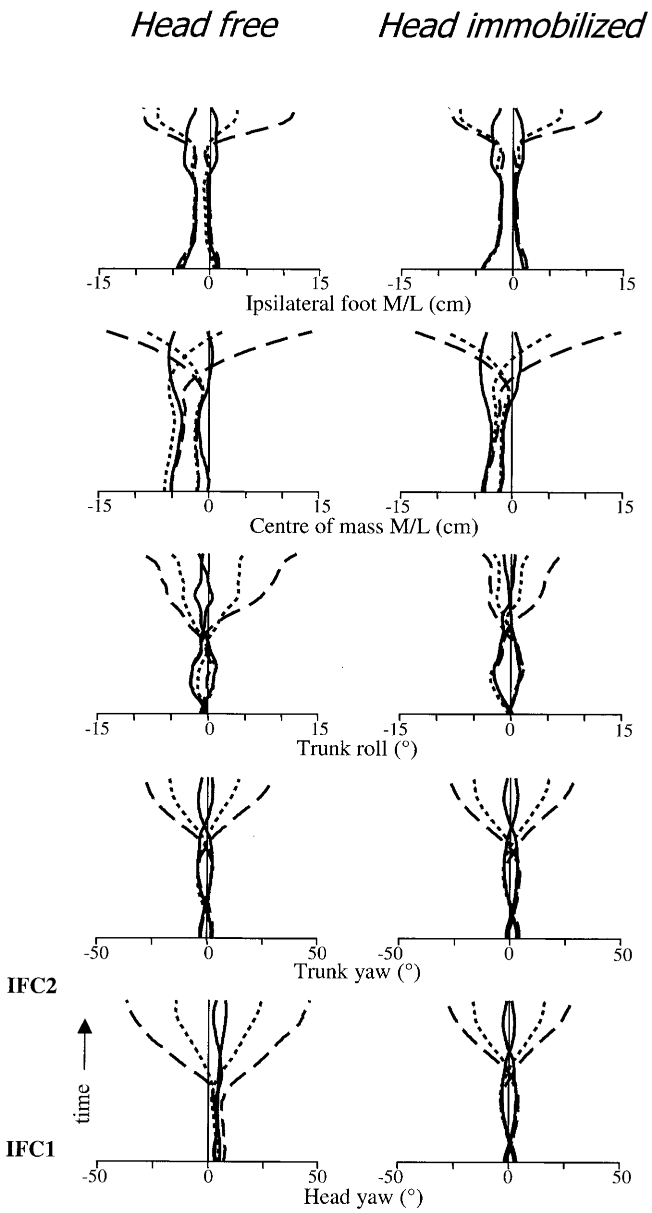

Fig. 2 Average profiles (five trials) for one individual of head yaw, trunk yaw, trunk roll, and ipsilateral foot and COM displacement in the M/L direction. Data obtained from individual trials were time-normalized with respect to the transition stride [first ipsilateral foot contact *(IFC1* on Fig. 1A) to the second ipsilateral foot contact (*IFC2* on Fig. 1a)] [*solid lines* data from control trials (0° turn), *dotted lines* data from 30° turn trials, *dashed lines* data from 60° turn trials, *black line* turns to the right, *grey lines* left turns, *left panel* averaged data obtained from the HF condition (head free), *right panel* averaged data obtained from the HI (head immobilized) condition]

Body translation

There are two main mechanisms by which COM can be accelerated in the new travel direction during the transition stride (see “Introduction”): (a) by altering contralateral foot placement prior to the turn step (reflected in adjustments to step width) and (b) by using the “hip strategy” to control the body pendulum in the swing phase of the turn step (reflected in trunk roll).

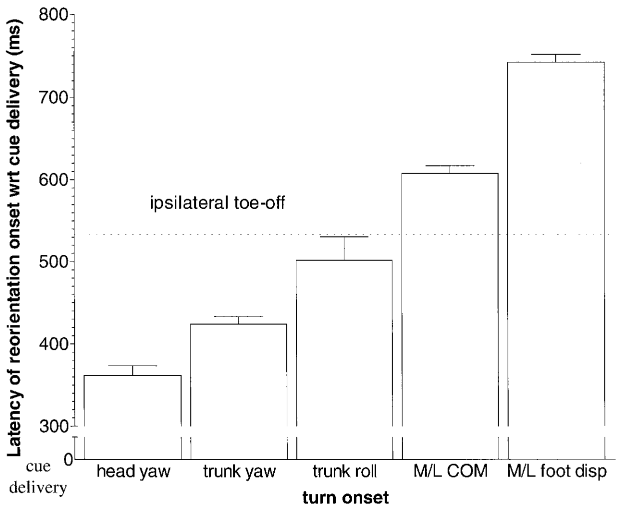

Fig. 3 Sequence of mean onset latency of reorientation for various parameters following a cue to turn. *Bars* represent head yaw, trunk yaw, trunk roll, M/L displacement of COM and M/L foot displacement, respectively. Cue delivery was at time 0 ms [*dotted line* mean onset latency of the turn step (onset of swing immediately prior to IFC2), *error bars* SEM in each case]

Step width

Step width (lateral distance between ankle markers) was measured and compared at three discrete times during each walk: at the start of the transition stride – IFC1 (at cue delivery), at the subsequent contralateral foot contact (CFC) and at the end of the transition stride (ipsilateral foot contact – IFC2). There was an interaction effect between the step event (IFC1, CFC2 or IFC2) and the required turn size on the magnitude of step width ($F_{(4,16)}$=48.8, P=0.001). Figure 4 shows the mean stance width for each turn magnitude and step event. There was a significant increase in stance width with turn direction. In particular there was a significant difference between the mean stance width at IFC1 and that obtained at CFC during turn trials. In other words, subjects increased their stance width by moving their contralateral limb in the opposite direction to the required turn during the transition stride. There were no significant differences between stance widths measured at CFC for 30° and 60° turns. However, there were differences at IFC2. Mean stance width was significantly greater for 60° turns than for 30° turns (T=–3.8, P<0.0005).

Trunk roll during transition stride

There was a significant interaction effect ($F_{(2,8)}$=13.09, P=0.003) between the size and direction of turn on the mean change in trunk roll during the transition stride (difference between values measured at IFC1 and

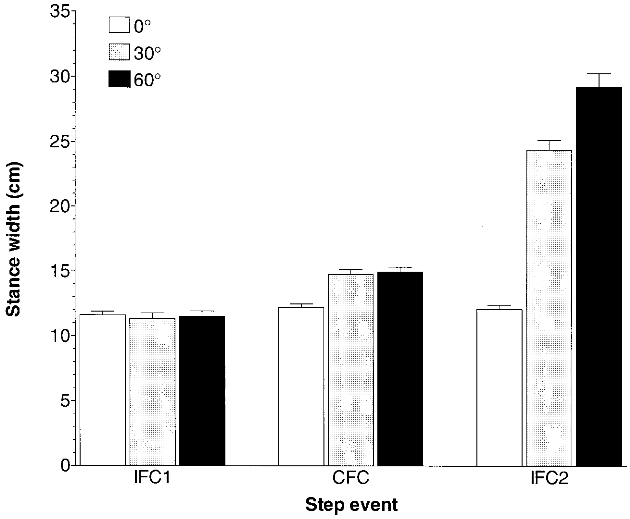

Fig. 4 Mean stance width for each step event during the transition stride (IFC1, CFC and IFC2) (*unfilled bars* control data, *grey bars* data for 30° turns, *black bars* show data for 60° turns)

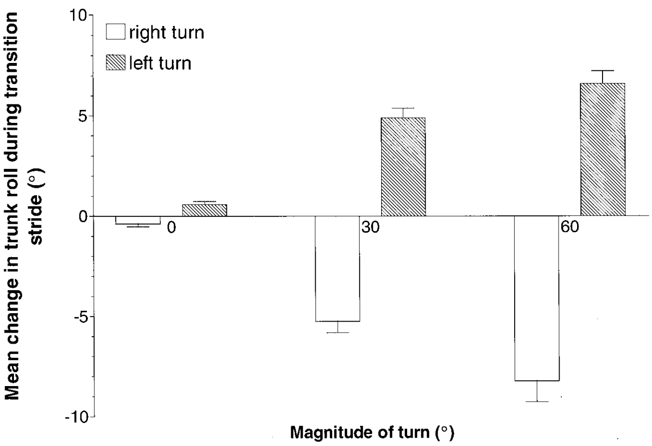

Fig. 5 Mean change in trunk roll during the transition stride (difference between values measured at IFC1 and IFC2 for each size and direction of turn). Negative values correspond to net leftwards trunk roll, positive values to net rightwards trunk roll (*filled bars* data obtained from left turn trials, *unfilled bars* data from right turn trials). Note that during turns to the left on average trunk roll increased towards the right and during turns to the right trunk roll increased towards the left)

IFC2). Figure 5 shows mean values for each size and direction of turn. During turns to the left on average trunk roll increased towards the right and during turns to the right trunk roll increased towards the left. Furthermore the larger the required turn the greater the mean change in trunk roll, e.g. the mean trunk roll (to the left) is nearly twice as large for a 60° turn to the right than the mean trunk roll for a 30° turn in the same direction.

To assess the degree to which changes in lateral COM location were associated with trunk roll (in the opposite direction), the change in trunk roll over the transition stride for each trial was plotted against the corresponding change in lateral COM displacement. This is shown in Fig. 6 together with the results of a least squares linear regression. A clear and significant correlation was obtained (r^2=0.78, P<0.0001). Therefore 78% of the variation in lateral COM displacement is attributable to variation in trunk roll magnitude.

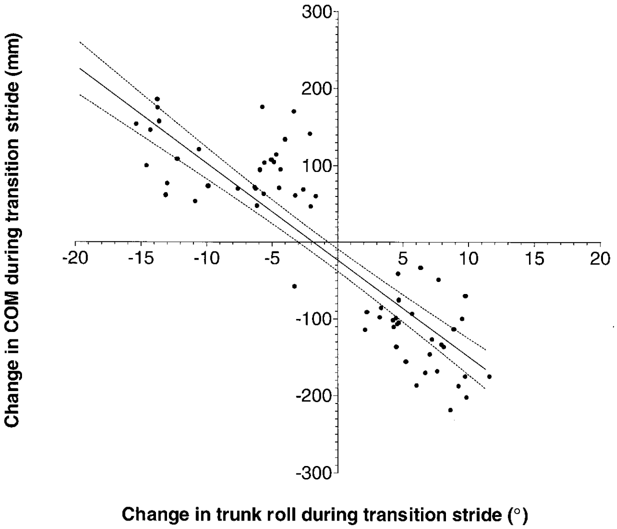

Fig. 6 Total change in M/L displacement of COM during the transition stride was plotted against the corresponding change in trunk roll over the same time period for each turn trial. *Superimposed lines* show the results of a least squares linear regression together with ±95% confidence intervals. The slope of the line (12.61±0.83) is significantly different from 0 (r^2=0.78, P<0.0001)

Stepping parameters: stride length

There was a main effect between stride length and turn magnitude ($F_{(2,8)}$=29.95, P=0.0002). The stride length progressively decreased as turn magnitude increased (straight: mean=124.6 cm, SD=6.6 cm, n=175; 30°: mean=117.7 cm, SD=6.7 cm, n=69; 60°: mean=107.3 cm, SD=7.0 cm, n=77).

Effects of head immobilization

Sequence of reorientation

The sequencing of reorientation onset for various body parameters (head yaw, trunk yaw, trunk roll, COM and foot displacement) following presentation of a direction-change cue showed an interaction effect between body parameter and head condition (HF or HI). In other words, fixing the head to the trunk resulted in a significant change to the sequence of orientation onset ($F_{(4,16)}$=3.24, P=0.0398,); mean head and trunk yaw onsets were now the same (as expected due to the experimental protocol) and trunk roll now followed COM (Fig. 7).

Table 1 Mean values and standard deviations of head yaw measured at IFC2 under the different experimental conditions. *Shaded rows* contain data for the head immobilized condition and *unshaded rows* data obtained from trials in which the head was free to move independently

Head constraint	Turn direction	Turn magnitude	Mean head yaw (°)	SD	*n*
HF	Left	0	–5.38	5.61	47
HI	Left	0	–2.54	3.79	42
HF	Right	0	–0.48	4.35	44
HI	Right	0	0.89	3.22	40
HF	Left	30	–24.31	3.37	20
HI	Left	30	–18.06	3.85	13
HF	Right	30	17.07	4.24	14
HI	Right	30	15.91	5.96	18
HF	Left	60	–42.18	6.75	13
HI	Left	60	–29.83	6.97	19
HF	Right	60	40.09	6.84	14
HI	Right	60	29.55	8.67	17

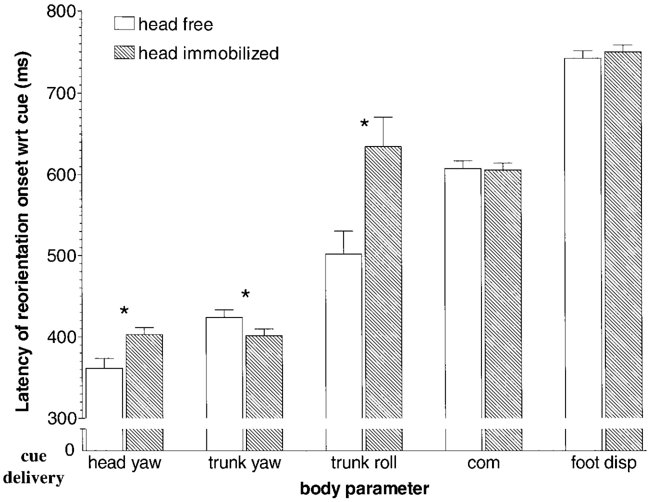

Fig. 7 Effects of head immobilization on the sequencing of reorientation onset for various body parameters (*filled bars* data obtained from the head immobilized condition, *unfilled bars* data from trials in which the head was free to move independently, *asterisks* significant differences between mean values)

Post hoc analysis (Bonferroni) revealed that mean onset of head yaw was significantly later to coincide with trunk yaw onset ($T=-2.82$, $P<0.005$) and mean trunk yaw onset was significantly earlier as predicted ($T=1.78$, $P<0.01$). Trunk roll onset latency was also significantly longer ($T=-2.87$, $P<0.005$).

Head and trunk yaw

There was an interaction effect between head constraint, turn size and turn direction conditions at IFC2 ($F_{(2,8)}=9.35$, $P=0.0143$) on the amplitude of mean head yaw. On average, the head was rotated significantly further in the turn direction by the end of the transition stride when the head was free than when it was immobilized. Table 1 shows the mean values and standard deviations of head yaw measured under the different conditions. No significant differences were found between mean trunk yaw values measured at IFC2.

Trunk roll

There was an interaction effect between size, head constraint and direction conditions on the mean change in trunk roll (IFC1 to IFC2) over the transition stride ($F_{(2,8)}=8.81$, $P=0.0123$). The change in trunk roll over the transition stride for each turn parameter is greatly reduced in the HI condition. Figure 8 shows the mean values of change in trunk roll for each size and direction of turn.

Head roll

Immobilizing the head had no significant effect on the values of mean head roll obtained for each size and direction of turn (despite the fact that amplitude of trunk roll was significantly reduced in the HI condition).

Trunk and head pitch

The mean head pitch (calculated using pooled data from IFC1, CFC and IFC2) was 9° in the HF condition (SD=3.4, $n=478$). The corresponding mean trunk pitch was 1.5° (SD=3.55, $n=478$). In the HI condition, both head and trunk pitch mean values were around 5° (head: mean=5.34, SD=4.2, $n=454$, trunk: mean=5.04, SD=4.17, $n=454$). Therefore, in the HI condition there was a compromise whereby the trunk (and therefore also the head) was rotated at an intermediate pitch angle between the HF head and trunk angles.

Centre of mass

There was a significant interaction effect between head constraint, turn size and direction conditions in the amplitude of lateral COM displacement over the transition stride ($F_{(2,8)}=5.60$, $P=0.0353$). Figure 9 shows the mean displacement of M/L for each experimental condition. Filled bars represent data obtained in the HF condition; empty bars show data obtained in the HI condition. Despite statistical significance, in each direction and turn condition differences between head conditions in COM

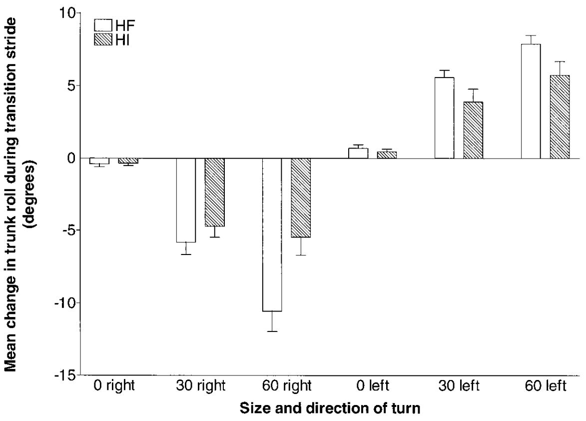

Fig. 8 Effects of head immobilization on the mean change in trunk roll during the transition stride (*filled bars* represent data obtained when the head was immobilized, *unfilled bars* data from trials in which the head was free to move independently)

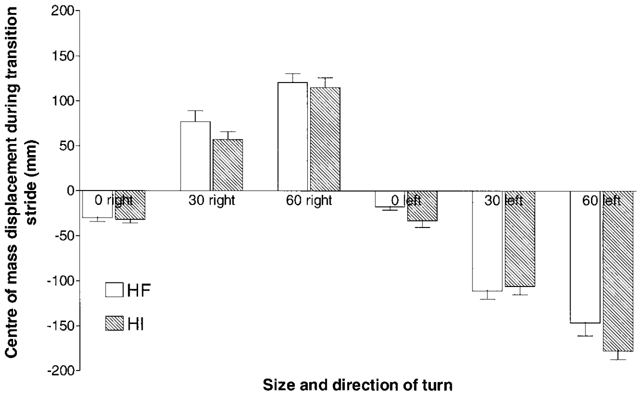

Fig. 9 Mean M/L displacement of COM during the turn stride for each experimental condition (*filled bars* data obtained in the HF condition, *empty bars* data obtained in the HI condition)

displacement were relatively small (range 2–30 mm). The largest difference was seen between data sets obtained from 60° left turn trials whereby the mean COM displacement was 30 mm more lateral during the HI condition than during the HF condition.

To assess the degree to which the linear relationship between lateral COM location and in trunk roll over the transition stride (observed in the HF condition) was affected by head immobilization, change in trunk roll for each HI trial was plotted against the corresponding change in lateral COM displacement over the transition stride. Again, a clear and significant correlation was obtained (r^2=0.63, P<0.0001, slope=–15.8). Therefore, despite the changes in trunk roll elicited by head immobilization there was still a significant linear relationship between these two variables. However, the correlation coefficient was notably smaller in the HI condition (HI=0.63: HF=0.78) and the slope of the regression line was larger (HI=–15.78±1.5: HF=–12.61±0.83).

Step width

There were no significant differences between step widths (IFC1, CFC and IFC2) measured under the HI and HF conditions. Immobilizing the head had no effect on contralateral foot placement prior to the turn step.

Discussion

Head direction and heading direction

The primary aim of this experiment was to test the hypothesis that anticipatory head movements towards the new travel path are proactively controlled by the CNS to provide a stable frame of reference for body reorientation. This was achieved by determining the sequence of body segment reorientation and lateral translation during a direction change paradigm and observing the effects of immobilizing the head (by fixing it to the trunk) on this sequencing. The temporal sequence of body reorientation observed in the head free condition of the present study was consistent with previous findings that the head starts to turn in the direction of travel before the reorientation of the rest of the body (Grasso et al. 1996, 1998; Patla et al. 1999). Our findings also show that, on average, onset of head reorientation preceded onset of lateral COM translation by around 250 ms: a value that is significantly smaller than that reported by Grasso et al. (1998) for subjects walking around a corner. However, the required magnitude of direction change was much larger (90°) and the participants always knew from the start of the trial that they would be required to turn. In an earlier experiment (Grasso et al. 1996), the authors reported that the head direction of subjects walking in circles systematically anticipated changes in the direction of locomotion by around 200 ms. This task, which required step-by-step adjustment to walking trajectory, produced similar time intervals between head reorientation onset and onset in change of direction of locomotion to those observed in the present study. Therefore it seems that the earlier that information describing the required direction change is received the larger the lead in head reorientation. This was described by Patla et al. (1999), who showed that head yaw onset (with respect to start of the transition stride) was significantly earlier by around 350 ms when the cue to turn was given at the start of the trial than when the cue to turn was given two steps in advance. However, the results presented here do differ from those previously reported by Patla et al. (1999). In the equivalent experimental condition in which participants were cued two steps before the required turn, the authors found that trunk roll onset occurred prior to that of head yaw onset. However, the experimental protocol used was quite different to the present one. Previously the cue lights describing the required route were attached to a board placed at eye level at the end of the straight path. Therefore participants were required to attend to (and so presumably fixated gaze on) a different location than the required travel direction to discover their route. Therefore it is possible that participants became aware that they were required to turn before they had time to use this indirect information to determine where in the environment they were to head towards and realign gaze (eye and head) accordingly. In the same experiment when participants were given their route information at the start of the trial, head yaw onset reorientation *did* precede the rest of the body. In the present experiment the light cues were placed in the same direction as the required travel route.

The second difference between protocols is that in the previous study participants were always required to turn in the same direction (to the right). Therefore, it is possible that participants made anticipatory modifications to facilitate body translation in the event that they would be required to turn. In the present experiment the subjects were not aware of the required turn direction prior to cue delivery. This is a much more realistic scenario in which both the magnitude *and* direction of the turn is determined in response to a visual description of the required travel path. Although the required turn direction was always towards the same side as the leg with which participants were instructed to start walking, participants did not behave as if they were aware of this. When debriefed at the end of the experiment all subjects reported that they did not notice this pattern. These major differences in protocol can account for the discrepancies between the present results and those reported previously.

Regardless of the differences resulting from using different experimental protocols, in all cases onset of head yaw reorientation with the new travel direction preceded that of changes in the direction of locomotion. These findings imply that proactive head alignment is a prerequisite for changing the direction of locomotion. However, they do not tell us whether proactive head realignment occurs as part of the gaze reorientation process or whether it provides an independent reference frame that is used to control travel direction. If head control is not independently important then one would predict that immobilizing the head, while still allowing the eyes to move, should have no significant effect on the normal steering strategy.

Effects of head immobilization

Immobilizing the head resulted, on average, in significantly earlier onset of trunk yaw reorientation with respect to cue delivery. This suggests that participants were attempting to compensate for loss of independent head mobility by changing the timing of their trunk reorientation thereby realigning the head with the new travel direction in a faster time. This indicates that aligning the head with the new travel direction prior to repositioning the rest of the body is an important component of the steering strategy and not simply a consequence of whole body reorientation, i.e. the head does not move first because it has lower inertial constraints than the trunk but rather the motor commands responsible for head reorientation are given earlier.

It should be stressed that the eyes were still free to move during the HI condition and therefore, theoretically, participants could still align gaze with the targets at the same time as during the HF condition. Although participants were occasionally presented with targets placed at an angle of 60° from the straight path (as measured at floor level), the actual angle of horizontal eye rotation required to transfer gaze between central orbit and a 60° cue light when it lit up was in the order of 40° (calculated for a 1.7-m tall participant with his/her leading foot on the trigger mat and their head aligned with the straight path at the moment of cue delivery). Therefore participants would need an oculomotor range of around 80° in order to foveate the eccentric cue lights moving the eyes alone. This value lies well within the accepted normal oculomotor range of around 90° (Burian and van Nooden 1974; Stahl 2001). Therefore, participants did not need to generate head movements in order to align gaze with the targets. The finding that significant changes were observed in the timing of trunk rotation when the head was immobilized lends strong support to the proposal that proactive head realignment is independently important for the control of steering control.

These results further suggest that head reorientation not only *anticipates* but also plays an active role in *dictating* future heading direction. In other words we propose that the head is not simply proactively moved to align with the estimated future orientation of the body but rather that proactive head alignment using vision provides an egocentric reference frame that is used to control body reorientation.

Immobilizing the head also had a dramatic effect on both temporal and amplitude characteristics of trunk roll. On average trunk roll onset was significantly later and amplitude significantly smaller in the HI condition than in the HF condition. However, there were no significant differences between mean values of *head roll* measured under the two conditions. This reflects the fact that compensatory head rotations (in all planes) are normally made in the opposite direction to the trunk rotations that occur during locomotion: the head is actively stabilized relative to space with a precision of a few degrees (Pozzo et al. 1990). These compensatory movements were not possible in the HI condition: any change in trunk roll caused a corresponding change in head roll. Therefore, the observed change in trunk roll behaviour may have served to minimize disruption to normal head and gaze orientation. Furthermore, the fact that onset of trunk roll occurs much later in the HI condition may reflect a strategy to delay disruptions to head orientation in the roll plane until appropriate head yaw alignment is achieved with the new travel direction. This is further evidence that independent control of head orientation in space is an important component of the CNS strategy used in changing direction of locomotion.

Role of eye movements

It is likely that the anticipatory head rotations are normally generated via coordinated eye and head movements as part of the process of reorienting gaze with the new travel direction. Grasso et al. (1998) investigated head and eye orientation in healthy volunteers walking along 90° corner trajectories, both in light and with eyes closed and found that head and eyes systematically deviated toward the future direction of the curved trajectory. Other instances of functional eye movements in complete darkness to remembered target locations have been documented during walking on stepping stones (Hollands and Marple-Horvat 1996, 2001) and during reaching movements of the hand (Enright 1995). It is hard to explain why people would make eye movements in complete darkness unless the oculomotor system provides information other than vision that is useful in guiding the movement of other body parts. Solomon and Cohen (1992) demonstrated that monkeys running in circles in both light and darkness produce coordinated eye and head movements that served to stabilize gaze. The authors suggested that “velocity storage” in the vestibular system, activated by the monkeys' ongoing movement, drives the compensatory eye and head movements. However, it should be noted that circular locomotion is a unique task that requires predictable step-by-step adjustment and the observed eye and head movements were compensatory, not anticipatory, in nature. Although it is hard to see how knowledge of current walking trajectory provided by “velocity storage” could play a role in generating the predictive eye and head movements that precede a change in walking trajectory, velocity storage does provide a possible mechanism by which the frame of reference for body repositioning is maintained during ongoing movement even in the absence of visual and vestibular input.

These results suggest that eye movement control plays an important role in the development and maintenance of a frame of reference for body movement even in the absence of vision. In light of these findings we propose a hierarchical schema whereby a visual image of a locomotor goal is first visually fixated via saccadic eye movements providing a gaze-centred frame of reference that can be used to align the head with the goal. Head realignment, in turn, provides the CNS with a head-centred frame of reference that is used to control body reorientation. Neurophysiological studies have identified “head direction cells” that fire selectively when the head is pointed in a specific direction in space in the thalamus and postsubiculum of rats (McNaughton et al. 1996) and in the primate presubiculum (Robertson et al. 1999). Therefore reorienting the head in the new travel can provide the CNS with both an allocentric and an egocentric reference frame that can be used to reorientate the rest of the body.

Knowledge of gaze behaviour during this walking paradigm would not only test our hypotheses regarding the related roles of the eye and head in steering control but also add to our general understanding of how vision is used to determine current and future heading directions. We have begun to explore these issues in recent experiments (Hollands et al. 2000).

Biomechanics of steering

The secondary aim of the present study was to investigate the control of body translation during direction change by accurately describing COM (derived from knowledge of full body kinematics), foot placement and trunk roll during a paradigm that introduced uncertainty about the required size and direction of the required locomotor adjustments. This is the first study to accurately describe COM during a steering task.

One way to move body COM is through muscle action at the hip and trunk, as described by Horak and Nashner (1986) in a study of participants' reactions to forward and backward platform perturbations. The body is controlled as a double pendulum with the legs and the upper body leaning in opposite directions resulting in the COM moving in the same direction as the hips. Patla et al. (1999) demonstrated that a M/L hip strategy was adopted by participants changing the direction of locomotion. This postural strategy was quantitatively described through measurements of the roll angle of the trunk.

The results of the present experiment demonstrate clearly that during a turn in either direction trunk roll was significantly increased in the opposite direction and that the larger the required turn, the greater the mean change in trunk roll. These findings are consistent with those of Patla et al. (1999) and support the proposal that a M/L hip strategy is used to control COM M/L acceleration. Further support is provided by the finding that a clear and significant correlation was obtained between amplitude of trunk roll and COM displacement over the course of the transition stride.

Since in the HI condition a change in the trunk roll profile occurred after onset of COM displacement, a strategy other than rolling the trunk must have initiated COM acceleration in the new travel direction. Our results demonstrate that this was achieved through increasing step width prior to onset of the turn step. Irrespective of head immobilization condition (HI or HF), on average, participants increased their stance width by moving their contralateral limb in the opposite direction to the required turn during the transition stride, thereby placing the contralateral foot in a more lateral position with respect to COM. Since the difference between COP and COM during walking swing dictates COM acceleration in the M/L direction (Winter 1995), this strategy serves to accelerate the COM in the desired turn direction, initiating body translation toward the new travel path. Therefore, during a change in the direction of locomotion, COM acceleration is achieved using a mixed strategy controlling both M/L foot placement and trunk roll angle.

There were no significant differences in the mean amplitudes of COM and foot displacement during the transition stride between the HF and HI conditions, in spite of the fact that the mean amplitude of trunk roll was significantly smaller and that onset of changes in trunk roll was significantly later. Additionally, immobilizing the head had no effect on either the latency of COM translation onset or on stance width measured at CFC. Therefore, the relative contribution of the hip strategy to COM control during steering is less clear than our other findings indicate. It is possible that coarse control of COM acceleration is provided by foot placement prior to the onset of the transition step and that trunk roll may be adjusted online in order to "fine-tune" COM trajectory during swing. Further investigation of the trunk roll and foot placement behaviour during steering is needed to quantitatively determine the specific contribution of each strategy to body translation. We can conclude, however, that both strategies play a role in accelerating the COM in the new travel direction. Patla et al. (1999) previously used knowledge of trunk roll to make inferences concerning COM behaviour. The results of the present study demonstrate that although there is a significant relationship between trunk roll and COM displacement the details of exactly how one relates to the other remain unclear. Therefore, one should exercise caution in using knowledge of trunk roll to describe COM behaviour.

Finally, although it is possible to change COM acceleration by increasing the mediolateral component of the push off thrust, our results demonstrate that, on average, onset of the change in M/L foot displacement occurred significantly later than toe-off. This observation can be explained by considering the biomechanics of normal straight path walking. In order to maintain forward momentum during walking humans must voluntarily fall forward at each step in order to accelerate their COM ahead of the base of support. At the start of each step the COM is accelerated towards the stance limb and follows a path along the medial border of the stance foot before moving in the direction of the swing limb (Winter 1995). This strategy ensures dynamic stability by effectively delaying M/L COM acceleration away from the stance limb until the swing limb is appropriately repositioned to accept body weight.

We propose that, when changing the direction of walking, the CNS moves COM laterally by positioning the body in such a way (by controlling step width and the body pendulum) that gravity causes it to fall in the required direction during the late swing phase of walking. This theory is supported by the results of Patla et al. (1991), who demonstrated conclusively that subjects were unable to change direction of walking within a step cycle. They were, however, highly successful when the cue to turn was given two steps in advance.

Conclusions

Head reorientation and stabilization, prior to changing the direction of locomotion, is so desirable that, when head mobility is compromised, both control of trunk reorientation (involving realignment of a large inertial mass) and control of body COM translation (observed as changes in trunk roll) are significantly affected. We propose that head reorientation plays an active role in dictating the future direction of locomotion and does not simply subserve gaze control, i.e. the body follows where the head leads.

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