The formation of trajectories during goal-oriented locomotion in humans. I. A stereotyped behaviour

Halim Hicheur, Quang-Cuong Pham, Gustavo Arechavaleta,
Jean-Paul Laumond, Alain Berthoz

August 20, 2007

Abstract

Human locomotion was investigated in a goal-oriented task where subjects had to walk to and through a doorway starting from a fixed position and orientation in space. The door was located at different positions and orientations in space, resulting in a total of 40 targets. While no specific constraint was provided to subjects in terms of the path they were to follow or the expected walking speeds, all of them generated very similar trajectories in terms of both path geometry and velocity profiles. These results are reminiscent of the stereotyped properties of the hand trajectories observed in arm reaching movements in studies over the last twenty years. This observation supports the hypothesis that common constraining mechanisms govern the generation of segmental and whole-body trajectories. In contrast, we observed that the subjects placed their feet at different spatial positions across repetitions, making unlikely the hypothesis that goal-oriented locomotion is planned as a succession of steps. Rather, our results suggest that common planning and/or control strategies underlie the formation of the whole locomotor trajectory during a spatially oriented task.

Introduction

When moving from a point A to point B in space, a great variety of trajectories can be taken. Even for a single (successful) trajectory, a theoretically infinite number of motor behaviours can be implemented by the motor system (a notion known as 'motor redundancy'). As the generation of a single motor

behaviour is associated with several levels of description, the elaboration of the motor command appears to be a particularly complex problem. Indeed, a great number of kinematic patterns (the velocity profiles of the segments involved in the task, for instance), dynamic patterns (the patterns of forces required to move these segments), myoelectric patterns (the muscular activation patterns producing these forces) or neuronal discharge pattern (the motor units innervating the muscles) may be combined for the generation of the successful motor behaviour (see Wolpert, 1997, for a review). In the case of multijoint movements, the problem becomes even more complex as the high dimensionality of the system results in an increased motor redundancy.

In contrast with this theoretical complexity, it has been experimentally observed that the arm reaching movements exhibit several motor invariants which are systematically reproduced by different subjects across repetitions. In this type of task, hand trajectories have been found to be highly stereotyped and particularly smooth. They are also marked by bell-shaped velocity profiles (for a review see Bullock and Grossberg, 1988) and by a specific relation between path curvature and hand velocity, known as the two-thirds power law (Lacquaniti et al., 1983). The observation that hand trajectories exhibit many invariants in different motor tasks (in contrast with much more variable joint angular profiles) led Morasso (1981) to propose that the central command underlying arm pointing movements is formulated in terms of hand trajectories in space. The kinematic nature of the control of arm movements was then associated with the notion of end-point movement control. However, the distinction between the different kinematic coordinates in which the CNS may encode (for instance) the direction of movement is still an open question (Soechting and Flanders, 1992).

The existence of such robust invariant features of motor execution was proposed as being the product of general principles governing movement execution. Among these principles, the optimal nature of motor control in biological systems was emphasized and minimizing cost functions were systematically used in computational approaches of movement learning and control (Todorov, 2004). These aspects are detailed in the companion paper.

In contrast with the numerous behavioural and computational studies devoted to the understanding of the trajectories in arm movements in humans, the generation and the control of whole-body displacements in space has received little attention. However, in addition to its purely sensorimotor component, locomotion also must be understood and analysed as a spatially oriented activity requiring navigational guidance. It immediately follows that characterizing locomotion at the level of trajectory is of crucial interest. Recent studies have assessed the vestibular contribution to the control of direction and distance during human locomotion (Glasauer et al.,

2002), multisensory contributions to the control of walking along a straight trajectory (Kennedy et al., 2003) and the nature of the visual strategies governing the steering of locomotion (Warren et al., 2001; Wilkie and Wann, 2006). Recently, we examined the principles underlying the control of locomotor trajectories by testing the hypothesis that common principles govern the generation of hand and whole-body trajectories (Hicheur et al., 2005b). In tasks where subjects had to walk along different types of curved paths, we observed a strong correlation between path curvature and walking velocity reminiscent of the power law observed for hand movements (Lacquaniti et al., 1983), but with significant deviations from the two-thirds exponent. We discussed the functional significance of our results by taking into account both the central and peripheral mechanisms that might account for the close relationships between path geometry and trajectory kinematics observed during human locomotion. It should be noted that these observations were restricted to a steering task where subjects had to walk along predefined paths.

Here, we investigated the generation of whole-body trajectories in a simple goal-oriented task. We wanted to examine whether the locomotor behaviour, analysed at the level of the step and at the level of the trajectory, exhibit motor invariants as observed in arm reaching movements. As locomotion is a motor activity mobilizing all the body segments, the locomotor systems are of a higher dimensionality and the redundancy of the motor solutions allowing the displacement of the whole body towards the spatial target is theoretically greater than that of arm movements. Nevertheless, a first reason explaining why such different movements (arm movements and locomotion) might share common principles was suggested by Georgopoulos and Grillner (1989). These authors proposed an analogy between hand reaching tasks and accurate foot placement during locomotion: in order to perform the visuomotor coordination in these two contexts, the same neural structures seem to be involved in the accurate positioning of the limb. The generation of the limb trajectory would thus be realised according to common mechanisms. In the case of goal-oriented locomotion, and following this suggestion, it is possible to hypothesize that the trajectory of the whole body could be built as a sequence of foot 'pointings' on the ground.

The purpose of the current study was to describe the spatial and temporal features of the locomotor trajectories. In particular, we tested the hypothesis that, as for hand movements, the body trajectories in space exhibit geometric and kinematic stereotypy while various motor strategies can be implemented for reaching the desired goal. To do this, we designed a goal-oriented locomotor task similar to a 'walking towards and through a distant doorway' situation. Subjects had to start from a fixed position and orientation in space and to walk throughout a door located at different positions and orientations

3

in space.

This first manuscript presents numerous quantitative analyses showing that human locomotor trajectories are generated according to common spatial or temporal criteria. In the companion paper (Pham et al., 2007), we propose a computational approach for modelling the principles underlying the generation of locomotor trajectories.

Materials and methods

Subjects: experimental setup

Six healthy male subjects volunteered for participation in the experiments. Each of them generated 120 trajectories corresponding to 40 spatial targets $\times$ 3 trials so that a total of 720 trajectories (6 subjects $\times$ 120 trials) were recorded for the experiment (parts of the recorded data were used for a study presented at the IEEE BioRobotics conference, Pisa, Italy, 2006; see Arechavaleta et al., 2006). Subjects gave their informed consent prior to their inclusion in the study. Experiments conformed to the Code of Ethics of the Declaration of Helsinki. The mean age, height and weight of the subjects were, respectively, 26.00 ± 2.76 years, 1.80 ± 0.07 m and 72.8 ± 6.15 kg. Three-dimensional positions of light-reflective markers were recorded using an optoelectronic Vicon V8 motion-capture system wired to 24 cameras at a 120 Hz sampling frequency. Subjects were equipped with 39 markers of which 10 were directly used for the analysis. Three reflective markers were fixed on a helmet ($\sim$ 200 g). The helmet was donned so that the midpoint between the two first markers was aligned with the head yaw rotation (naso-occipital) axis. Thus the line which indicates the head orientation passed through these two markers (Head Forward F and Backward B). To assess the body displacement in space we used the midpoint between left and right shoulder markers, which were located on left and right acromions, respectively (see Hicheur et al., 2005b). Two markers were located on the pelvis (left and right anterior superior iliac spines) and two markers were located on each foot: they were placed at the top of the foot (subjects were allowed to wear shoes) between toes 2 and 3 (1 is the big toe), and on the heel at the same height as toe marker. These markers were used for detecting the step events (explained below). We defined head, trunk, pelvis and trajectory reference frames as illustrated in Fig. 1A. Forty targets were used for the experiment: the target consisted of a doorway which was placed at a specific (x, y) position in the motion-capture space with an orientation α (Fig. 1B and E). Four markers were rigidly fixed to the target and were recorded during the whole

duration of all trials. This allowed us to verify that the position and the orientation of the door (for a given condition) were the same for all subjects.

Protocol

The aim of this protocol was to study the locomotor trajectories generated by different subjects and to test whether these trajectories display properties similar to those reported for hand reaching movements.

Subjects had to start from a fixed position in the laboratory and walk toward and through the doorway (Fig. 1A). To verify that all subjects began the task in the same conditions we asked them to begin their walk 1 m before crossing the start line and with a body initial orientation which had to be approximately orthogonal to the X-axis of the laboratory. They were then completely free to choose their walking speed and no specific restriction was placed on them regarding the path to follow. They were not asked to stop walking after entering the doorway because this instruction could have biased their behaviour a few steps before reaching the door. Rather, they were left free either to directly come back to the starting position or to walk in the laboratory for several seconds before coming back to the starting position. Typically, subjects walked straight for a few metres (about four steps) after passing through the doorway before returning to the starting position. The experimenter stopped recording the movement of the subject a few metres after he passed through the door. The angular displacement of the body in space induced by the different orientations of the doorway (see Table 1) ranged between -150 and +150°. As subjects were carefully monitored during the session, the average distance ($\pm$ SD, across all the recorded trajectories) between the actual and the imposed initial positions was 3.0 $\pm$ 2.5 cm, the average distance between the actual and the imposed final positions was 3.2 $\pm$ 2.2 cm, the average absolute difference between the actual and the imposed initial orientations was 9.6 $\pm$ 7.9° and the average absolute difference between the actual and the imposed final orientations was 5.9 $\pm$ 4.4°.

Analysis

In this study, we wanted to understand whether whole-body trajec tories are organised according to common spatial or temporal criteria across different subjects during goal-oriented locomotion. We there fore focused on two levels of description of the locomotor behaviour Firstly, we examined the geometric and kinematic properties of the locomotor trajectories in order to characterize the spatial control of the whole-body movement. This approach can be associated with the notion of end-point trajectory control. Secondly,
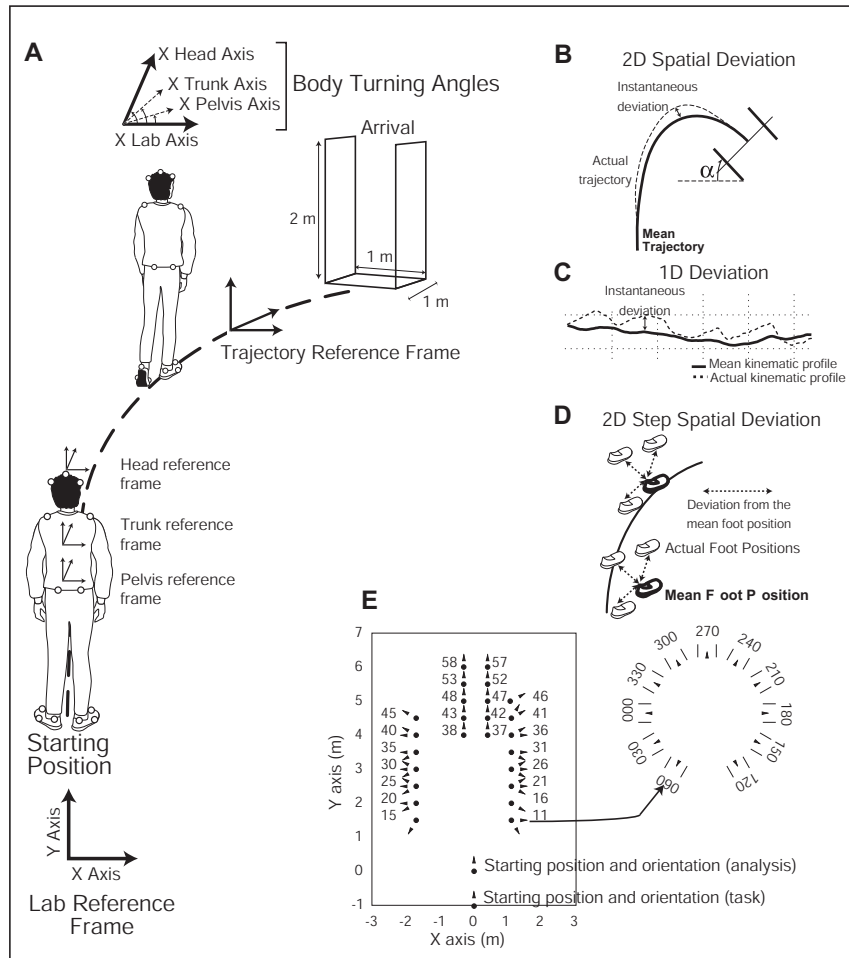
5

Figure 1: (A) Experimental protocol: subjects had to start from a fixed position in the laboratory and to walk through a distant doorway. The position and the orientation a of the door were the two manipulated parameters and 40 combinations, position and orientation, were tested. (B) The spatial deviation of the actual trajectory from the mean trajectory was measured as the distance integrated over time between the mean (across subjects and trials) and the actual trajectories. (C) The variability of the velocity or turning profiles (kinematic profile) was measured as the deviation between the actual kinematic profile and the mean kinematic profile (across subjects and trials). (D) For different repetitions of a given condition, the spatial dispersion of the foot positions around the mean foot position was measured. (E) Spatial disposition of the 40 tested targets (see also Table 1). Each target position is represented by a small black disk. The possible target orientations for each target position are indicated by arrows.

6

we studied in detai the succession of locomotor cycles. This approach tests whethe locomotion is planned as a succession of discrete cycles from which emerges the global trajectory.

Categorization and computation of the trajectories

The tested trajectories were classified into four categories according to the amount of body turn they required: quasi-straight trajectories (ST), and trajectories of low (LC), medium (MC) and high (HC) curvature (see Table 1).

The total distances travelled by subjects ranged between 4.50 ± 0.25 m (across subjects and trials) for the nearest target and 9.38 ± 2.54 m for the furthest target. However, in order to compare the different trajectories with precise criteria, the final calculation of the travelled distance was performed between the instant t0 where subjects crossed over the X-axis and the instant t_1 where they entered the doorway, according to the task requirements (the final position was calculated at the instant where the body crossed over the middle of the door). This method yielded values of trajectory length between 2.03 ± 0.08 and 6.46 ± 0.01 m (across subjects and trials). The individual values (across subjects and trials, for each tested target), in terms of trajectory length, duration and average walking speed, are presented for the 40 targets according to each category in Table 1.

After this procedure, and for each target, the trajectories were time-resampled so that for all subjects and trials of the same target, $t_0 = 0$ and $t_1 = 1$. This was done in order to compare the actual trajectories to the mean trajectory. The number of frames (N_f) of the re-sampled trajectories was chosen individually for each target across trials, as the N_f contained in the trial (trajectory) with the shortest duration. Thus, all the trajectories recorded for a single target had the same N_f. A Matlab routine (Mathworks V6.5 ®) was then implemented in order to re-sample the individual trajectories according to this parameter: this routine consists of a linear interpolation of the new (re-sampled) trajectory using N_f as the number of frames contained in this re-sampled trajectory.

After the 40 trajectories were sorted in the four categories, all the quantitative parameters (see below) were computed separately for each target. A mean value for each of these parameters was then calculated for each group of trajectories across the 10 targets ($\times$ 6 subjects $\times$ 3 trials) ranked in each category.

Spatial variability of the trajectories

In order to examine the similarity in the time courses and forms of the trajectories produced by the different subjects, we computed the mean trajectory (across subjects and trials) and calculated, for each trajectory toward a given target, the deviation from the mean trajectory; this gave an index of the spatial variability in the trajectories (see Fig. 1C).

The averaged trajectory $(x_{av}(t), y_{av}(t))$ was calculated as follows:

$$\left(x_{av}(t) = \frac{1}{N} \sum_{i=1}^{N} x_i(t), \quad y_{av}(t) = \frac{1}{N} \sum_{i=1}^{N} y_i(t) \right) \tag{1}$$

where N is the number trials recorded for this target.

The trajectory deviation (TD) was computed as the sum of the instantaneous distances between the averaged $(x_{av}(t), y_{av}(t))$ and the actual $(x_i(t), y_i(t))$ trajectories, and was calculated as follows:

$$\mathrm{TD}(t) = \sqrt{\frac{1}{N} \sum_{i=1}^{N} (x_i(t) - x_{av}(t))^2 + (y_i(t) - y_{av}(t))^2} \tag{2}$$

The averaged and maximal deviations between the actual trajectories and the mean trajectory are denoted ATD and MTD, respectively. This procedure was repeated for each of the 40 tested targets.

Spatial variability of the foot placements

We examined the pattern of foot positions from the beginning of the task until the subjects reached the goal. To this purpose, we first detected the successive steps performed by subjects before computing the variability in the foot locations $(x_f(t), y_f(t))$ across the different repetitions of the same subject. We used heel-strike and toe-off events for defining steps (Hicheur et al., 2006). These events were derived from the time course of heel and toe Z-position profiles and correspond to the local minima of these two signals. We considered one step as the interval separating two successive heel strikes of the same foot and computed the foot positions at these particular events.

A first type of intersubject variability was observed at the level of the foot placements during the task because of the anatomical differences between the subjects (as presented before, they had different heights and this resulted in different step lengths). In the present analysis, we did not consider the intersubject differences (which considerably increased the magnitude of the variability; not presented) in the foot placement but we calculated, for each

subject and for a particular target, the variability of the foot positions across the different repetitions. This was done in order to compare the pattern of the successive positions of the feet across trials. Typically, a subject performed M to M+1 steps to reach the goal. In order to compare the spatial position of the feet across trials, we selected the first M steps and calculated, for each step, the dispersion around the mean foot position. This was quantified in exactly the same way as described for the parameters previously presented. However, the measure here was discrete because we did not integrate the variability continuously throughout the trajectory but rather measured it at the different step instants (see Fig. 1B). In order to compare this spatial variability in the foot positioning with that of the whole-body trajectory, we also expressed the spatial dispersion of the foot as a percentage of the step length. The spatial deviation from the mean trajectory presented above was also expressed, at this stage of the analysis, as a percentage of the trajectory length.

The foot position variability computed at the step instants is given by the parameter FD where

$$\text{FD} = \sqrt{\frac{1}{M} \sum_{j=1}^{M} (x_{\text{feet}.j} - x_{\text{av.feet}.j})^2 + (y_{\text{feet}.j} - y_{\text{av.feet}.j})^2} \qquad (3)$$

where M is the number of steps produced by a subject in order to reach the target, and where $(x_{\text{feet}.j}, y_{\text{feet}.j})$ and $(x_{\text{av.feet}.j}, y_{\text{av.feet}.j})$ are the actual and mean foot positions, respectively. We computed, as for the previous parameters, the averaged and the maximal dispersion of the foot (left and right) around the mean foot position (AFD and MFD, respectively). This analysis was performed for each subject and we then averaged this value across subjects.

Kinematic variability: velocity profiles and turning behaviour

In addition to the spatial variability of the locomotor behaviour analysed both at the trajectory and step level, we performed a quantitative examination of the velocity and turning profiles variability throughout the trajectory, across subjects and trials.

Velocity profiles

The instantaneous tangential velocity of the body was computed according to the formula $v(t) = \sqrt{\dot{x}(t)^2 + \dot{y}(t)^2}$. In order to measure the variability of

the velocity profile among the different subjects and trials, we computed the mean velocity profile $v_{av}(t)$ and calculated the deviation from the mean velocity profile VD and its associated averaged and maximal deviations (AVD and MVD, respectively), following the same procedure as the one used in equations 1 and 2. However, here the deviation accounts for a one-dimensional variability (Fig. 1C).

Turning behaviour: head, trunk and pelvis rotation in space

Also of interest was the variability of body rotation in space among subjects and trials. The calculation of the parameter $h(t)$ corresponds to the angle formed by the shoulder segment and the laboratory X-axis: it provides a measure of the time course of the body turning behaviour in a space-fixed reference frame. We computed the parameters BD (body deviation) and the parameters ABD (average BD) and MBD (maximal BD) in order to examine the extent to which subjects produced similar turning behaviours. We performed the same measurements for the head and pelvis rotation profiles and this basically resulted in similar qualitative observations. Thus, the measure of variability is provided for the trunk rotation profile only (Fig. 7E).

Anticipatory head behaviour

During human locomotion when the body turns along a curved path, the head angle anticipates the instantaneous walking direction. In the present study, we quantified the variability of this head anticipatory behaviour across subjects and for the different targets. This was done in order to address the motor implementation of the trajectory (e.g. how the head drives the steering behaviour). Indeed, it was found that this anticipatory head behaviour remains in the blindfolded condition (Grasso et al., 1996; Prévost et al., 2003) (see also Hicheur et al., 2005a, for a review) and that spatial, rather than temporal, cues drive the anticipatory head motion. In this last study, it was observed that subjects initiated 90° turns at a constant distance from the point of maximum curvature rather than at a constant time. Here, we performed a similar analysis but testing turns of different amplitudes (see Table 1) in order to examine whether this observation holds across the different tested targets. We calculated, for all the recorded trajectories (and 40 associated targets), the time and the distance before the turn initiation. The turn initiation was measured as the instant where the head maximally deviates from the walking direction provided by the tangent to the trajectory. We then computed the time τ and the distance d at which this instant occurred. These parameters referred to the instant and position where the

10

target was reached and are expressed as percentages of trajectory length or total movement duration. The amplitude of the maximal head deviation was also calculated for all trajectories.

Statistical analysis

We performed repeated-measurements ANOVA and t-tests with the Statistica 5.1 software package (Statsoft ®) in order to compare the variability calculated across the four categories of trajectories. The mean and maximal deviations from the averaged trajectory were compared in order to quantify the effect of the trajectory's curvature magnitude on the variability of the behaviour. The level of significance of the tests was set at $P < 0.01$. A second set of tests was devoted to comparing the spatial variability expressed either as percentages of the trajectory length or as percentages of the step length (see previous section). The variability parameters were computed for the 720 recorded trajectories (however, because we lost foot markers in a few trials, the real number of trajectories included in the different statistical tests was 713) and a total of 4385 steps were analysed (2161 left steps and 2224 right steps).

  While the trajectories were categorized according to the turn amplitude (see Table 1), we performed a second series of statistical tests in which we analysed the effects of the path length and the door orientation (and its required turn amplitude) as well the interaction between these two variables (path length $\times$ turn amplitude) for all the tested targets, irrespective of the categories presented in Table 1 (the targets being defined in terms of position and orientation). To this purpose, we performed a multiple regression analysis for the three independent variables mentioned above (path length, turn amplitude and interaction term) across the 713 recorded trajectories. This was done in order to detect potential significant effects of these independent variables on a particular dependent variable (e.g. the mean walking speed, the mean deviation from the average trajectory, the mean deviation from the mean foot position, the mean deviation from the average velocity profile, and the maximal head deviation and its spatial and temporal occurrences; see above).

Results

For all the 40 trajectories we observed very similar geometrical forms of the locomotor paths and velocity and body rotation profiles across the different repetitions and subjects. This indicates stereotypy at the level of the spatial,

kinematic and 'behavioural' attributes of the locomotor trajectories. In contrast, we observed much more variability when the locomotion was analysed at the level of the foot positions in space.

Spatial stereotypy of the locomotor trajectories

As illustrated in Fig. 2 (for all the tested targets) and in Fig. 3A (for four typical targets), we observed that the locomotor trajectories produced by the different subjects across different repetitions were very similar. We measured the spatial stereotypy as the ATD and MTD. As illustrated in the histograms presented in Fig. 3B, the ATD and MTD were < 10 and 17 cm, respectively. We observed that the larger the turn amplitude, the greater the deviation from the mean trajectory ($F_{3,531} = 58.15$, $P < 0.01$ for the ATD and $F_{3_531} = 66.39$, $P < 0.01$ for the MTD). However, it is remarkable that even for the highly curved trajectories the ATD was ~ 10 cm. The results from the multiple regression analysis, performed for all the tested orientations, confirmed the previous result observed at the level of the different categories of trajectories. Indeed, the turn amplitude was found to significantly affect the ATD ($F_{1,711} = 136.71$, $P < 0.01$). The path length was not found to significantly affect this parameter ($F_{1,711} = 1.20$, $P > 0.01$) but an interaction between the path length and door orientation was observed ($F_{1,711} = 185.86$, $P < 0.01$).

Spatial variability of the foot placement

While all subjects generated stereotyped locomotor trajectories, their behaviour was much more variable when examined at the level of the step. Part of this variability can be related to the anatomical differences between subjects (see Materials and methods).

In the present section, we calculated various parameters of the stepping behaviour within trials of a single subject (intrasubject analysis): this was done in order to quantify the spatial dispersion of the foot positions independently of the anatomical intersubject differences.

The foot positions at the step instants are presented for all subjects and for four typical trajectories in Fig. 4A. This figure shows the contrast between the foot placements and the corresponding trajectories plotted on the right side of the same figure. The different types of spatial dispersion of the feet are illustrated in Fig. 5A. In most of the configurations accounting for this variability we observed that subjects, when performing different trials of the same target, generated a similar trajectory but located their feet at different positions. The global body trajectory in space remained unaffected because
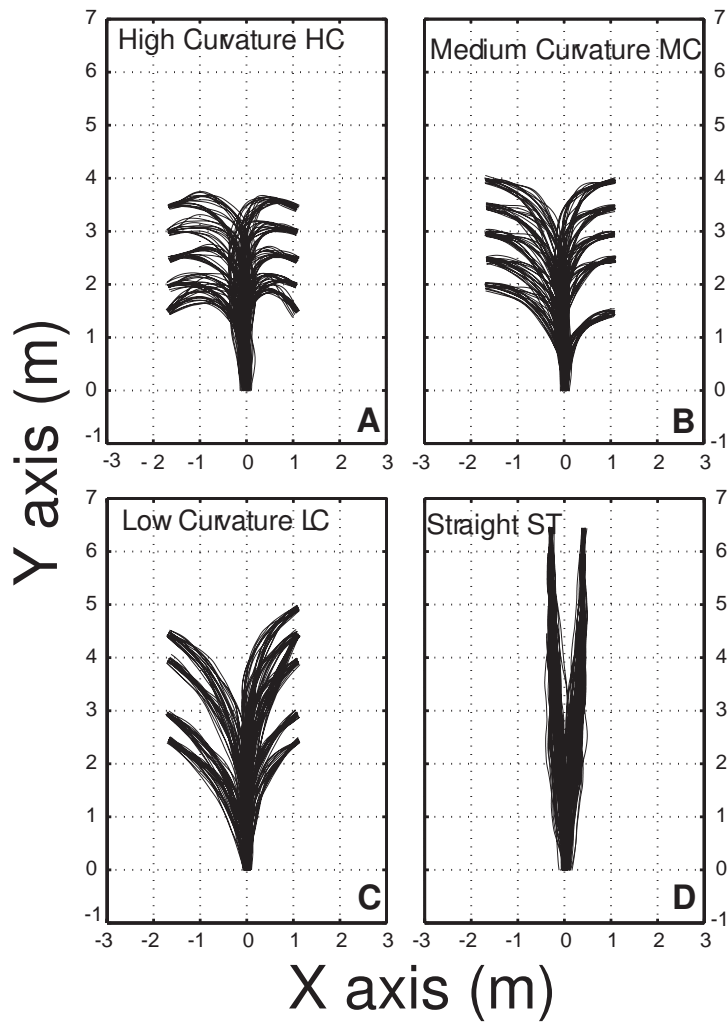
Figure 2: (A-D) Trajectories for all the tested targets, classified into four categories: high (HC), medium (MC) and low (LC) curvatures and quasi-straight (ST) trajectory groups. Ten targets were tested for each category. Note that for a single target position, two orientations might have been tested (see Table 1 and Fig. 1D for the target positions for which two orientations were tested).
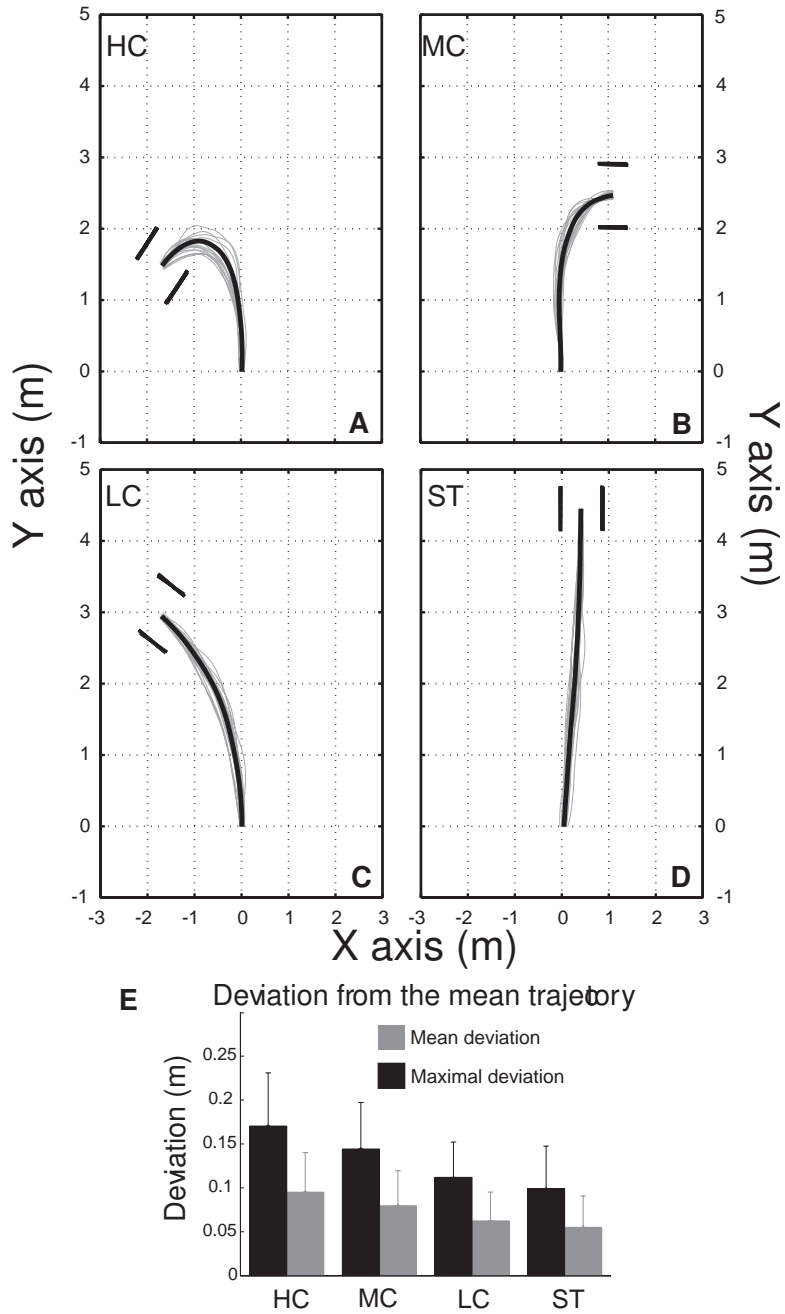
Figure 3: (A-D) Actual (grey) and mean (black) trajectories computed for four typical targets. (E) Mean and maximal deviations from the mean trajectory calculated for each target category.

14

every deviation (from one trial to another) of a given foot towards the right or the left of the X-axis was compensated for by a displacement of the position of the contralateral foot in the opposite direction (this was observed in most of the subjects; see Fig. 5A-D).

Another source of foot positioning variability across repetitions is due to the fact that subjects alternated between the left and the right foot for initiating their walk. Even after taking this into account, the foot positions (independently of whether we considered the left or the right foot) still exhibited some spatial dispersion across successive paths (see Fig. 5B and C). The trajectories presented in Fig. 5B thus combine these two sources of variability (e.g. anatomical differences and alternating right-left foot). Finally, we observed in a minority of cases that stereotypy in the body trajectories in space was associated with somewhat similar foot positioning across successive paths (see Fig. 5D).

The quantification of these observations is presented in Fig. 4C, in which the spatial dispersion of the foot positions across repetitions is plotted for the four categories of trajectories. The spatial dispersion of the feet around the mean foot positions was not dependent upon the type of trajectory ($F_{3,492} = 0.93$, $P > 0.01$ for the ATD and $F_{3,492} = 3.34$, $P > 0.01$ for the MTD) and ranged between 14 and 22 cm. The results from the multiple regression analysis, performed for all the tested orientations, confirmed that the variability in the foot placements was not dependent on the turn amplitude or on the path length. Indeed, the turn amplitude was not found to significantly affect the deviation from the mean trajectory ($F_{1,702} = 0.96$, $P > 0.01$; note that 10 trials were not analysed because of lost foot markers; see Materials and methods). The path length was also not found to significantly affect this parameter ($F_{1,702} = 0.10$, $P > 0.01$) and no interaction between the path length and door orientation was observed ($F_{1,702} = 0.76$, $P > 0.01$).

These absolute values of foot spatial dispersion obtained at the level of the step were twice as high as the ATD with respect to the mean trajectory presented in Fig. 3. This greater variability is even more evident if these parameters are expressed either as percentages of the step length or as percentages of the trajectory length (see histograms in Fig. 5E and F). The statistical significance of these differences is particularly strong ($F_{1,164} = 647.04$, $P < 0.01$ for the left foot dispersion around the mean left foot position compared with the spatial deviation around the mean trajectory, and $F_{1,172} = 711.06$, $P < 0.01$ for the right foot spatial dispersion compared to the deviation from the mean trajectory). The same observations hold for the maximal deviation parameters ($F_{1,164} = 457.03$, $P < 0.01$ for the left foot spatial dispersion compared to the deviation from the mean trajectory and $F_{1,172} = 693.89$, $P < 0.01$ for the same comparison performed with the right foot).
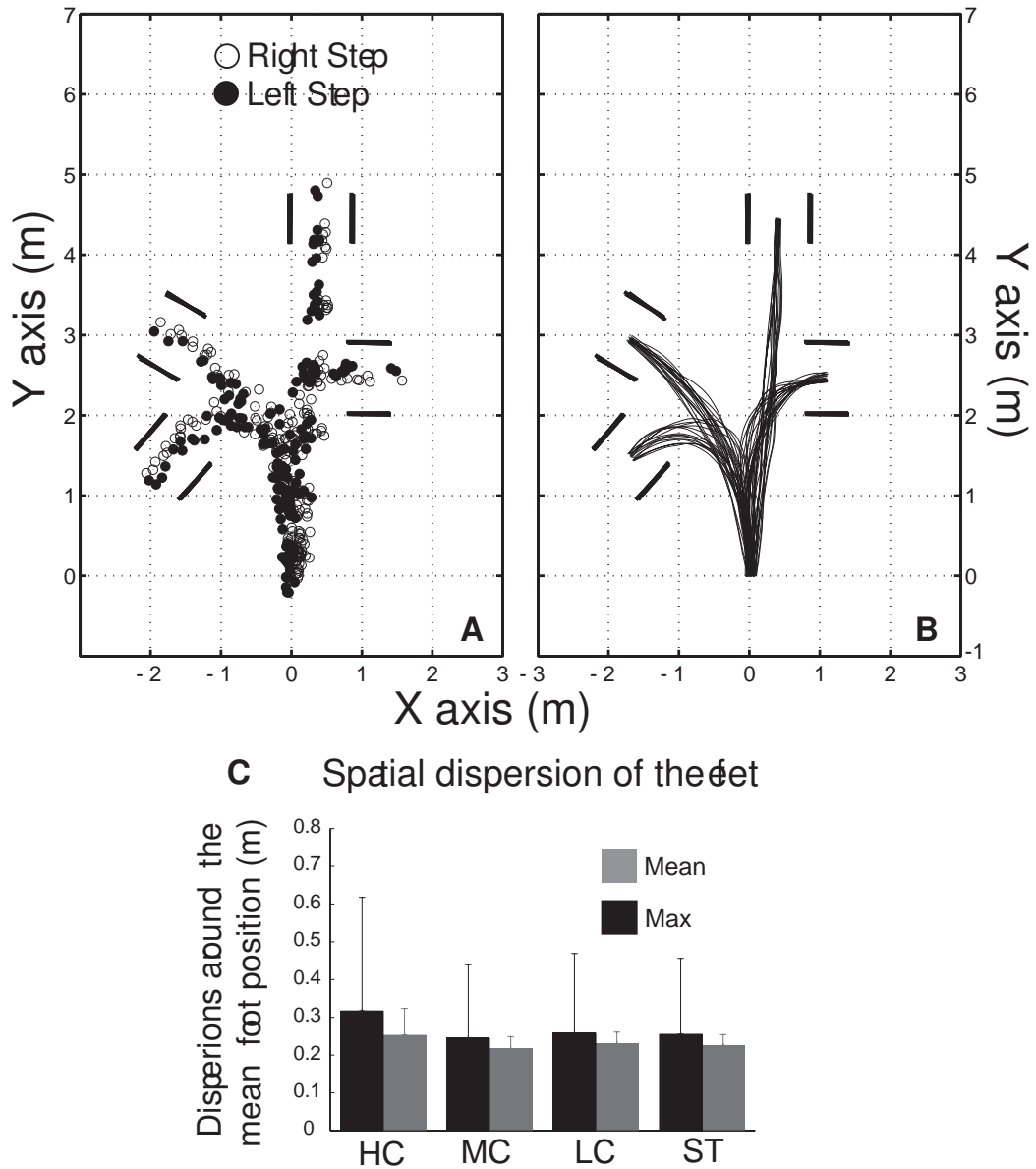
15

Figure 4: (A) Foot location for four typical targets (same ones as in Fig. 3) for all subjects and trials and (B) corresponding trajectories: note the similarity between the trajectories and the more variable foot placements. (C) Mean and maximal spatial dispersion (in m) of the foot positions calculated for each target category.
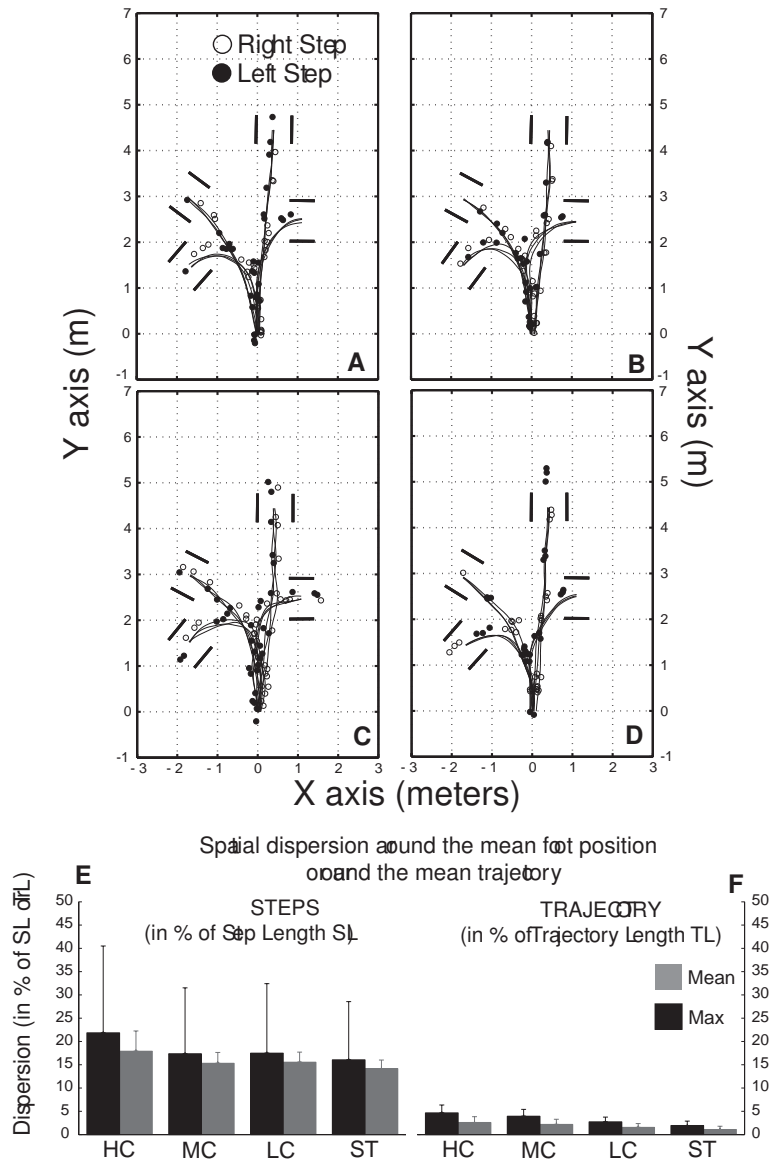
16

Figure 5: (A) Foot locations at the step instants (the left and right foot locations are plotted for each of the three consecutive trials) and corresponding trajectories for a particular subject and four typical targets. Note that the number of steps for completing the task may vary from M to $M + 1$ for the same target (see Materials and methods). (B-D) Same plots for three other subjects. Note the similarity between the trajectories and the greater variability of the foot locations in space. (E) Spatial dispersion of the actual foot locations around the mean foot positions expressed as percentages of the step length. (F) Spatial dispersion of the actual trajectories around the mean trajectory expressed as percentages of the trajectory length.

17

Taken together, these results show that for a simple goal-oriented task subjects generated very similar trajectories but using different foot placements: this indicates that the locomotor trajectory is unlikely to be constructed as a succession of 'foot reaching'. In the subsequent sections, we tested whether the motor implementation of the trajectory (in terms of either how subjects modulated their walking speed or how they changed their body orientation along the trajectory) presented stereotyped features across subjects.

Kinematic stereotypy

Velocity profiles

In addition to the spatial proximity of the locomotor trajectories (which corresponds to the static component of the trajectory, that is, the locomotor path), we observed that the velocity profiles were very similar across subjects and repetitions. This is illustrated in Fig. 6A-D, in which are plotted the velocity profiles produced by the different subjects for the four categories of trajectories. The histograms quantifying the proximity between these profiles are presented in the bottom of the same figure (Fig. 6E). In contrast with what was observed for the spatial attribute of the trajectory, VD (the mean deviation from the average velocity profile; ~ 0.10 m/s) was not affected by the length or the amount of body turn induced by the trajectories ($F_{3,531} = 2.33$, $P > 0.01$ for the mean deviation from the mean velocity profile and $F_{3,531} = 1.50$, $P > 0.01$ for the maximal deviation). The multiple regression analysis failed to reveal any interaction effect (turn amplitude-path length) on the prediction of the MVD ($F_{1,711} = 4.72$, $P > 0.01$). VD significantly varied according to the turn amplitude ($F_{1,711} = 6.81$, $P < 0.01$) but was not significantly affected by the path length ($F_{1,711} = 1.24$, $P > 0.01$). However, this analysis revealed that the mean walking speed as well as the minimum of walking speed significantly ($P < 0.01$) varied with both the turn amplitude and the path length (the interaction effect turn amplitude-path length was also significant; $P < 0.01$).

Turning behaviour: head, trunk and pelvis rotation in space

Although subjects generated similar velocity profiles, the time course of their turning behaviour could have been different throughout the trajectory execution. However, as depicted in Fig. 7A-D, the subjects generated very similar turning behaviours as quantified by the continuous reorientation of the body in space (head, trunk and pelvis angles with respect to the X-axis
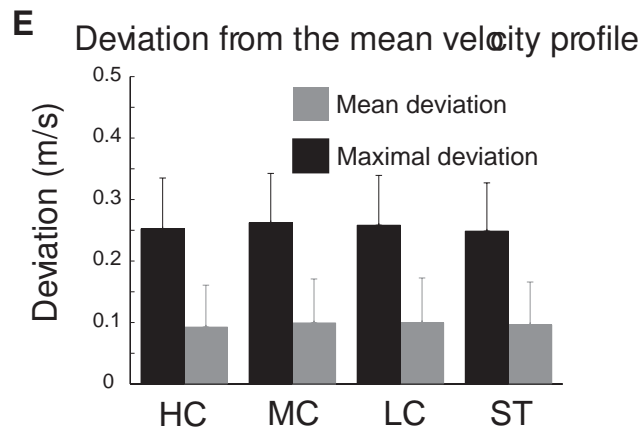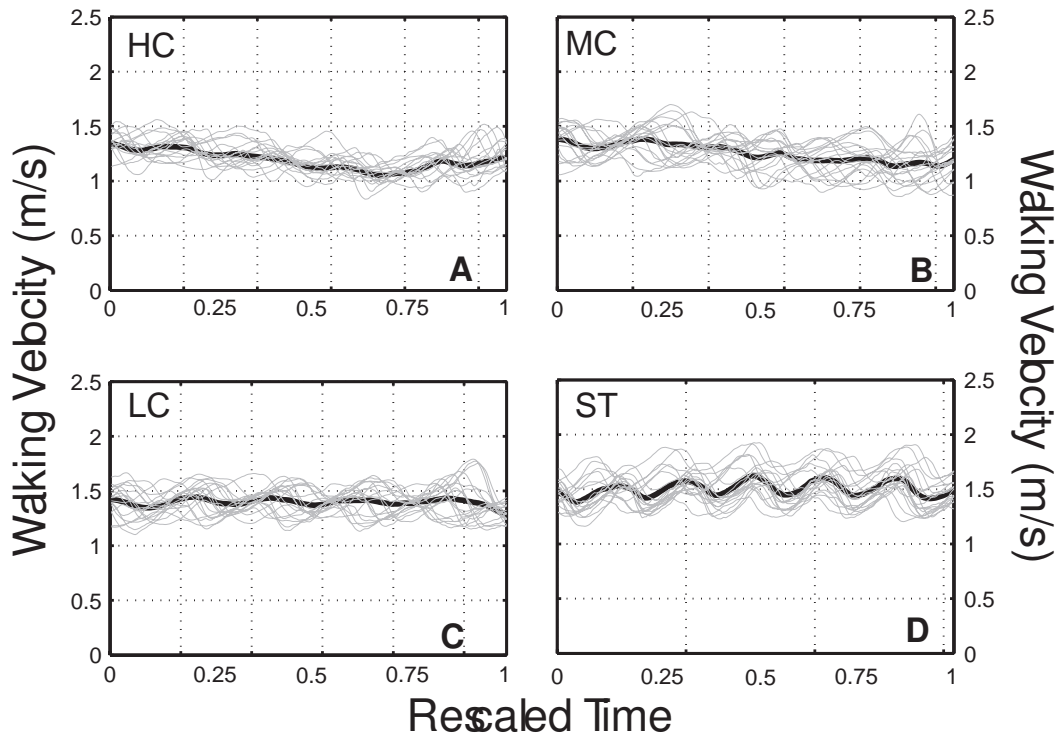
Figure 6: (A-D) Actual (grey) and mean (black) walking velocity profiles computed for four typical targets (same ones as in Fig. 3) (E) Mean and maximal deviations around the mean velocity profile calculated for each target category.

of the laboratory reference frame). We observed that the variability of the body rotation in space (calculated from the trunk segment; see Materials and methods) was $< 6°$ on average and $< 15°$ at most (Fig. 7E).

A statistically significant difference was observed between the four categories of trajectories ($F_{3,531} = 107.87$, $P < 0.01$ for ATD and $F_{3,531} = 116.57$, $P < 0.01$ for MTD): the more curved the trajectory the greater the deviations from the mean body rotation profile (however, only a $6°$ difference from the mean body rotation profile was observed for the most curved trajectory on average). This profile is similar to the one observed for ATD; although these deviations were small at the absolute level, they can be explained as follows. The amplitude of the turn induced by the curved trajectories was of a decreasing magnitude and reached its minimum for the near-to-straight walking. By normalizing the deviation with respect to a fixed value corresponding to the amplitude of the turn induced by the target orientation (this amplitude was calculated as the angle between the door and the Y-axis of the laboratory), the pattern of an increasing variability with an increasing curvature of the trajectory can be replaced by a deviation from the mean body rotation profile which is comparable across the four categories of targets. This possible explanation also holds for the deviation from the actual trajectory. However, we prefer to report absolute rather than relative measurements because this describes the way the magnitude of curvature affects the variability of the locomotor behaviour.

In any case, and for all the trajectories, the very small magnitude of variability in the computed spatial and kinematic profiles provides evidence for a stereotyped behaviour during a goal-oriented locomotor task in humans.

Anticipatory head behaviour: time and distance before turn initiation

In agreement with previous observations we observed that, for the trajectories analysed here, the head direction anticipated the actual walking direction. This was observable both when computing the head deviation in the trajectory reference frame (Fig. 8A-D) and when computing the head, trunk and pelvis orientation profiles in the laboratory reference frame (Fig. 7A-D). In the second case, the head orientation was systematically in advance of the trunk and pelvis orientation (in the case of left turns, this is illustrated by the fact that the curve corresponding to the head orientation is ahead of those of the trunk and pelvis, and vice versa), confirming that the head drives the steering of the locomotion.

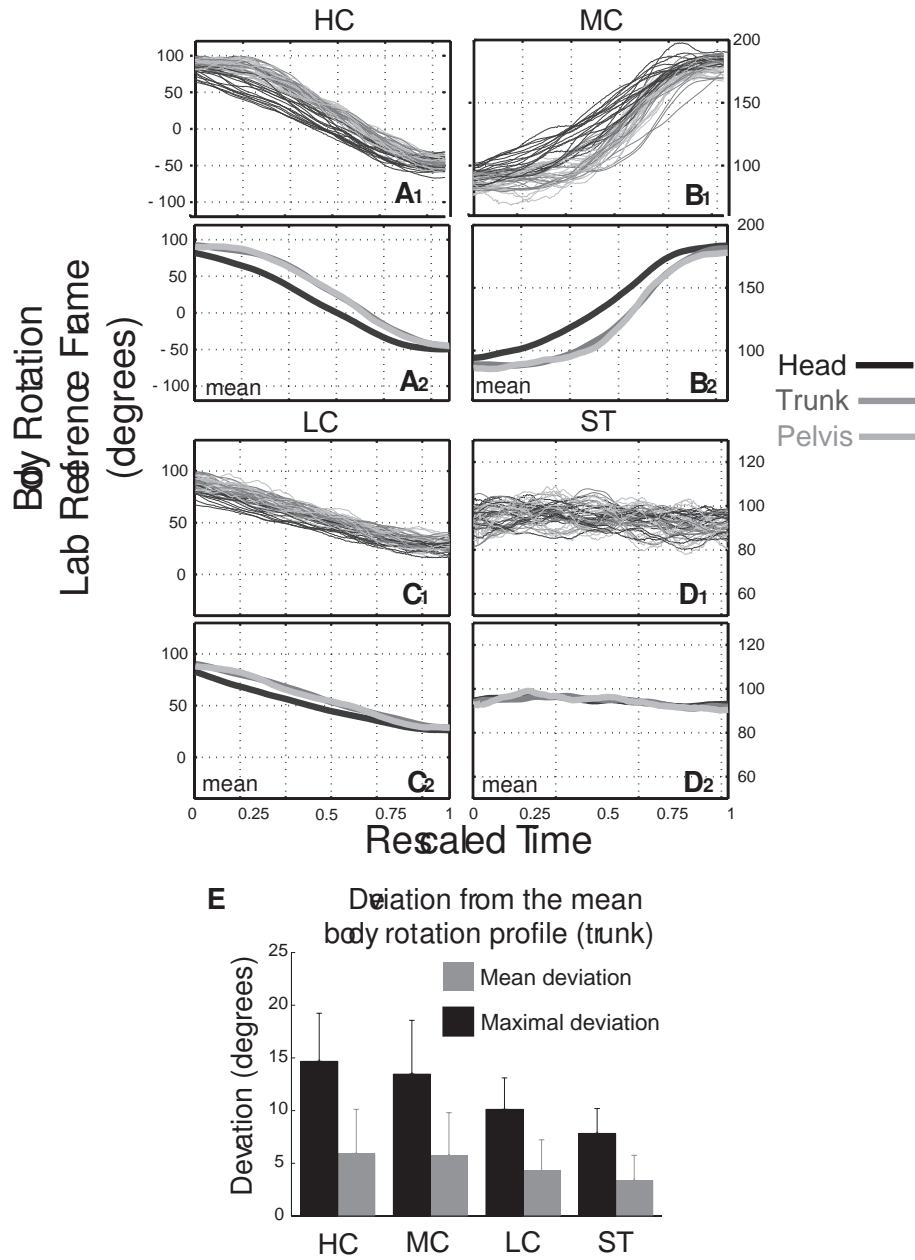The amplitude of the maximal head angular deviation is presented in

Figure 7: Actual (A1, B1, C1 and D1) and mean (A2, B2, C2 and D2) body rotation profiles (head, trunk and pelvis rotations in the horizontal plane of the laboratory reference frame) computed for four typical targets (same ones as in Fig. 3) (C) Mean and maximal deviations around the body rotation profile calculated for each target category.
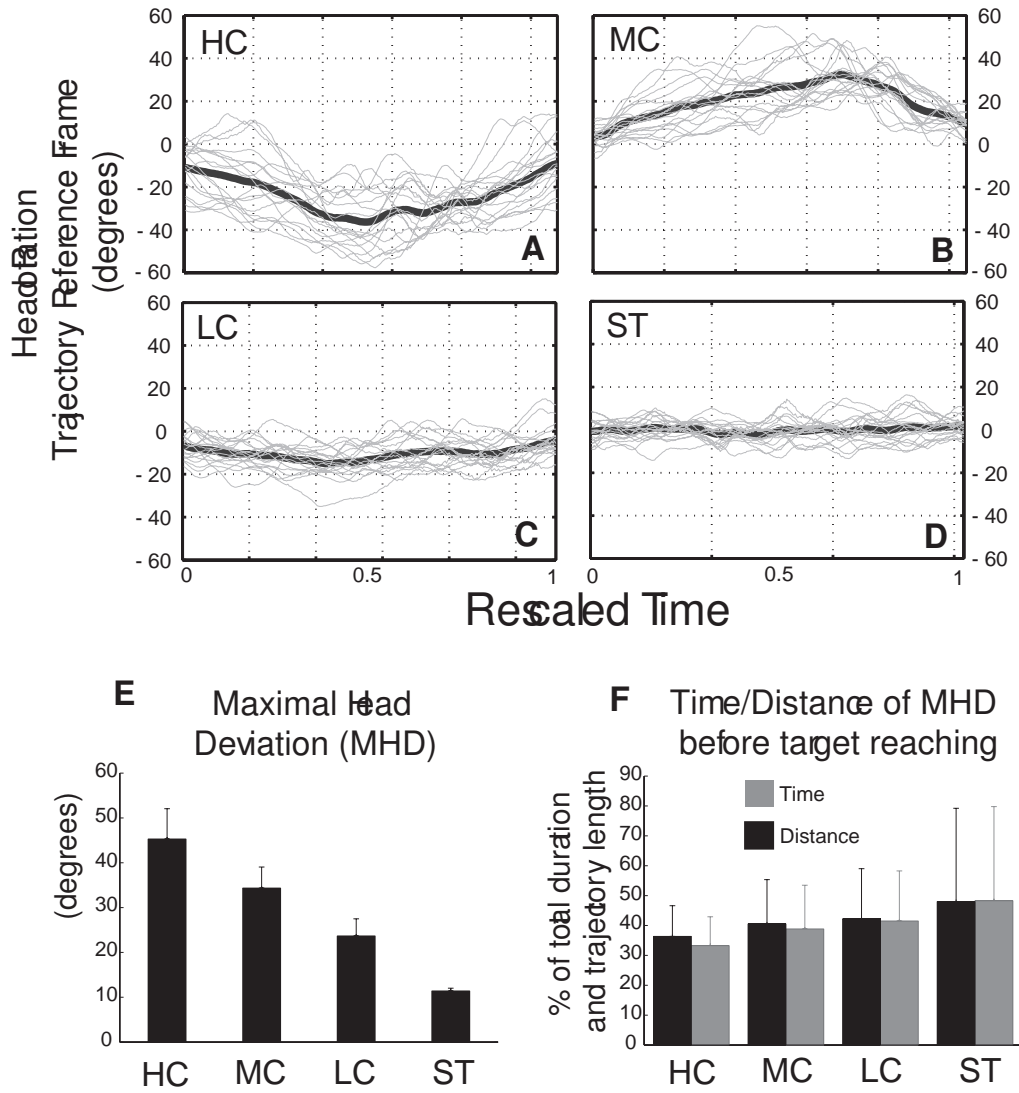
Figure 8: (A-D) Actual (grey) and mean (black) head rotation profiles (trajectory reference frame) computed for four typical targets (same ones as in Fig. 3) (E) Turn initiation: magnitude of the maximal head deviation MHD calculated for each target category. (F) Time and distance from the target (as percentages of the total duration and as percentages of the trajectory length, respectively) at which the head maximally deviates (note the greater variability with the decreasing curvature).

Fig. 8B. In the case of straight-ahead walking, the maximal head deviation reached $\sim 10°$, which corresponds to the natural oscillations induced by step alternation. The maximal head deviation (from 23 to $45°$) was greater for the more curved trajectories ($F_{3,531} = 2158.6$, $P < 0.01$). The multiple regression analysis revealed a statistically significant interaction effect (turn amplitude-path length) on the prediction of the maximal head deviation (MHD; $F_{1,711} = 1008.27, P < 0.01$). A statistically significant difference was also observed when individually comparing the different path lengths ($F_{1,711} = 154.75$, $P < 0.01$) and the different door orientations ($F_{1,711} = 1421.06$, $P < 0.01$) for all the recorded trajectories.

The instant and the distance at which the maximum of head deviation occurred also inform about the spatial and temporal sequencing of the steering (re-orientations in space) of the whole body. These parameters are expressed either as percentages of the total movement duration or as percentages of the trajectory length (Fig. 8B). The greater variability in these parameters was obtained for the near-to-straight trajectories; this illustrates the fact that no systematic anticipatory behaviour of the head was observed for this condition. In contrast, we observed that the maximum head deviation ranged from $\sim 42\%$ (for the least curved trajectory) to $\sim 36\%$ (for the most curved trajectory) of the trajectory length and movement duration.

Interestingly, the variability in these measurements was also a function of the type of trajectory: the more curved the trajectory the less the variability (and the more systematic the behaviour). We were not able to distinguish whether subjects initiated their turn at a specific spatial position rather than at a specific instant before the target. Nevertheless, we observed that, on average, the head maximal rotation always occurred before completing the first half of movement. Furthermore, our results show that the turn-amplitude parameter dictated the time and the distance (before the target was reached) at which the head maximally anticipated ($F_{3,531} = 72.415$, $P < 0.01$ when comparing this maximal head deviation between the different groups of trajectories). The multiple regression analysis revealed a statistically significant interaction effect (turn amplitude $\cdot$ path length) on the prediction of the spatial occurrence of the MHD only ($F_{1,711} = 12.53$, $P < 0.01$). This was associated with a statistically significant effect of the turn amplitude ($F_{1,71}1 = 7.30$, $P < 0.01$) but no significant effect of the path length was observed ($F_{1,711} = 4.09$, $P > 0.01$; note that $P < 0.04$). A different result was observed at the level of the temporal occurrence of the MHD: the effects of both the turn amplitude ($F_{1,711} = 1.97$, $P > 0.01$) and of the interaction term (path length-turn amplitude; $F_{1,711} = 5.16$, $P > 0.01$; note that $P < 0.02$) were not significant. In contrast, the path length was found to significantly affect the temporal occurrence of the MHD ($F_{1,711} = 7.72$, $P > 0.01$). Taken

23

together, the results of these statistical comparisons showed that the turn initiation (as quantified by the MHD) was a function of both the turn amplitude and the path length. Furthermore, the path length seemed to mainly affect the instant where the turn was initiated while the turn amplitude tended to preferentially affect the distance from the target at which the turn was initiated.

Discussion

When a subject is asked to go through a distant doorway (starting from a known position and body orientation in space), he has several possibilities for planning and executing the movement or the sequence of movements allowing him to reach this goal. At least two strategies can be used: one consists of placing his feet at specific positions on the ground, implementing step-by-step a trajectory of the whole body. Alternatively, the subject can plan the whole trajectory and implement different movements allowing him to follow this trajectory. While these two possibilities are not exclusive and might be combined in some way (for instance in the presence of an unexpected obstacle) we observed that, in a simple goal-oriented task, on repeated trials subjects reproduced very similar trajectories, albeit using much more variable spatial foot positioning (this greater variability was evident from both the intersubjects and intrasubject analysis). The observation of a stereotypy of the locomotor trajectories is particularly striking because locomotion mobilizes all body segments. This results, at a theoretical level, in a greater dimensionality of the motor system and the corresponding number of motor solutions (redundancy) compared to the motor apparatus involved in the generation of arm movements.

Indeed, we observed that for reaching the same target the subjects did not position their feet at the same positions in space. In contrast, the paths they followed were very similar in terms of both spatial and kinematic variability.

The spatial control of locomotion: path stereotypy and step variability

We believe that these observations are the first reported for human locomotion and are partly reminiscent of the results published more than 20 years ago regarding hand reaching movements (e.g. Morasso, 1981). However, locomotion is a special case because it supposes the integration of two levels of understanding and description of the movement. The first is related to the stepping level and is not necessarily coincident with the second one, which

is related to the task for which it is necessary to consider the locomotor trajectory as a whole. While our results show that it is unlikely that locomotor trajectories are constructed as succession of 'foot pointings' we observed, in agreement with the concept of dimensionality and redundancy evoked in the Introduction, that various combinations of foot placement (originating from different leg movements) are performed by subjects in order to reach the target. However, it should be noted that in avoidance tasks where the foot placement was constrained it was shown that minimal displacement of the foot from its normal landing spot was validated as an important factor for selecting alternate foot placement (Patla et al., 1999). In contrast, in our simpler and less constrained environment the kinematic invariance observed at the level of the trajectory might be taken as evidence for a spatial control of locomotion where the spatial accuracy of the body displacement in the environment is explicitly specified in the motor planning and execution. While this statement raises the question of which control variable can be used at this stage, we demonstrate here that the control of the trajectory is expressed in terms of space-related displacement of the body rather than foot-related displacement. In a similar vein, based on the observation that a significantly greater variability was observed in the joint angular displacements than in the hand trajectories (for different tasks), Morasso (1981) proposed the hypothesis that the central command is formulated in terms of trajectories of the hand in space. In our case, the different combinations of foot displacements may also be associated with different motor strategies allowing the steering of the body along the planned trajectory of the body in space.

Stereotypy in the steering behaviour: a top-down scheme for the control of locomotion

It must be emphasized that the stereotypy of the locomotor behaviour reported in this study not only concerns the spatial aspect (the geometry of the locomotor path) but also characterizes the temporal component of the locomotor trajectory. Indeed, the velocity profiles as well as the body turning profiles were also very similar across subjects throughout the trajectory. This means that not only did the subjects follow similar paths but they also regulated their steering behaviour along the trajectory in a similar manner. This is not contradictory with the observation of the variable foot positioning because the motor behaviour here is considered at the trajectory level. However, as revealed by the multiple regression analysis, the individual and combined effects of the door orientation (and its required turn amplitude) and of the door position (and its associated path length) on the spatial vari-

ability of the trajectories and on the velocity profiles should be noted here. While the variability of these parameters is < 20cm for the MTD and < 0.10 m/s for the MVD for all the tested targets, the observation of an increasing variability with the turn amplitude and the path length may restrict our observations (of stereotyped trajectories and velocity profiles) to a particular size of the locomotor space. Further experiments might help in testing how stereotyped would be trajectories generated in larger environments.

For straight trajectories, the velocity was nearly constant while it decreased with the increasing magnitude of the turn. An interesting observation here is that the velocity variations were very similar across subjects: subjects could have abruptly decelerated their walking velocity when negotiating the turn or they could have reduced their velocity early before entering the turn, then maintaining a constant low velocity during the turn. However, they all decreased their velocity continuously and progressively, resulting in smooth locomotor trajectories (this aspect is studied at the theoretical level in the companion paper).

The analysis of the steering behaviour confirmed the initiatory role of the head for the steering behaviour: a top-down temporal sequencing of the body reorientation, beginning first with the head then followed by the trunk and the pelvis, was observed. While this organization could not be observed for the nearly straight trajectories, the anticipatory deviation of the head towards the future walking direction was found to be a function of the magnitude of the turn; the greater the turn, the larger the head deviation and the later (and the closer to the target) occurred the maximum of head deviation. However, for this last parameter we were not able to distinguish between the spatial and/or temporal cues that drive the head deviation but we did observe that there was a combined effect of the turn amplitude and the path length on the spatial and temporal occurrences of the maximal head deviation. As mentioned earlier, it is unlikely that the formation of the whole-body trajectories would emerge from a planning strategy based on the foot positioning, given the variability of the latter parameter. Thus, the body displacement in space might be expressed, at the planning level, either by the head or the trunk movement in space.

As the head contains both the vestibular and visual systems, and is linked to the remaining parts of the body by the neck which contains proprioceptive sensors, the head movement in space might be a critical variable for the steering of locomotion. This has been formalized by Imai et al. (2001) as the gravito-inertial acceleration (GIA) vector and it corresponds to the sum of linear accelerations acting on the head. These authors showed that orienting mechanisms direct the eyes, head and trunk movements to tilts of the GIA in space during curved walking. In addition to these orienting mechanisms,

the stabilization of gaze through vestibulo-ocular and vestibulocollic reflexes (resulting in a stabilization of the visual scene) might facilitate the smooth changes in the body reorientations in space (as observable in Fig. 7A-C) from the turning profiles where continuous, rather than abrupt, direction changes characterize the steering behaviour).

Independently of the availability of sensory information, spatial memory abilities might also significantly contribute to the control of the locomotor trajectories. Here, we restricted our experimental protocol to the simplest goal-oriented task and we did not manipulate either sensory information or spatial memory, so it would be interesting to further examine their contribution to the stereotyped behaviour of subjects in a future study where perturbations might be applied to the displacement of the subjects. Taken together, all these observations confirm that the head serves as a mobile reference frame for the spatial control of the whole-body displacement in space (see Pozzo et al., 1990; Hicheur et al., 2005a, for a review).

Common principles may govern the formation of both hand and locomotor trajectories

Locomotion, which involves all the body limbs, is part of the basic motor repertoire of humans. However, the dimensionality of the locomotor system is higher than that of the motor system responsible for the hand movement, making it difficult to define the conceptual link between the system that controls the hand movement and that which controls the whole-body movement.

Recently, however, Papaxanthis et al. (2003) showed, by studying upward and backward movements performed in the sagittal plane, that similar planning strategies for whole-body and arm movements might be implemented by human subjects. While they discussed their observations with respect to how gravitoinertial forces are integrated in the elaboration of the motor command for hand and whole-body movements, here we would like to discuss possible similarities in the spatial control of hand and whole-body movements. Indeed, we studied a spatially oriented locomotor task and suggested an analogy with hand reaching tasks. For hand movements, the possibility that the control of movement is realised according to the end-effector coordinates in space was proposed both in experimental observations and theoretical studies (see Introduction). For instance, it was proposed that the CNS learns reaching movements by minimizing the variance of the final end-effector position (Harris and Wolpert, 1998). At first glance, it would be inappropriate to speculate that locomotion is controlled on the basis of a final position of the body in space; indeed, because locomotion is most often performed in temporal and

spatial scales greater than those of hand movements, the formation of the locomotor trajectory could well be planned in a piecewise manner.

This possibility of segmenting the planning of the locomotor trajectories in a sequential manner has also been proposed by Viviani and Cenzato (1985) for hand drawing movements. The authors based this interpretation on the observation that one parameter in the velocity-curvature relationships (the so-called one-third power law), the velocity gain factor, was modulated at particular points separating geometrically distinct parts of the trajectory. We recently observed such modulation when studying human locomotion along predefined complex trajectories (Hicheur et al., 2005b), suggesting that the control strategy or a number of the control parameters of the body displacement in space are tuned according to some spatial criterion which still remains to be identified. In our study, the possibility that a segmentation process is present might be associated with the observation that subjects first walked along a straight line before initiating a turn in order to reach the goal. However, for a given target we were unable to detect whether the subjects initiated their turn at a specific (invariant) distance or time before reaching the target, so the hypothesis of a segmented control of locomotion cannot be supported using these parameters. It should be noted that, even for hand movements, this hypothesis has been considerably challenged recently (Richardson and Flash, 2002).

In our opinion, the main reason that could explain the analogy between the planning of either hand or whole-body trajectories is that, during motor learning, the CNS plans and regulates the movement by choosing optimal solutions. This possibility, which has been amply tested in many experimental situations and theoretically formalized for arm reaching movements (see Todorov, 2004, for a recent review), may be studied in a systematic way in animal and human locomotion (the topic of the companion paper).

Acknowledgements

Abbreviations

ABD, average BD; ATD, averaged TD; AVD, averaged VD; BD, body deviation; FD, foot position variability; HC, high curvature trajectories; LC, low curvature trajectories; M, number of steps to reach the goal; MBD, maximal BD; MC, medium curvature trajectories; MHD, maximal head deviation; MTD, maximal TD; MVD, maximal VD; Nf, number of frames; ST, quasistraight trajectories; TD, trajectory deviation; VD, deviation from the mean velocity profile.

References

D. Bullock and S. Grossberg. Neural dynamics of planned arm movements: emergent invariants and speed-accuracy properties during trajectory formation. *Psychol Rev*, 95(1):49–90, Jan. 1988. ISSN 0033-295X.

A. P. Georgopoulos and S. Grillner. Visuomotor coordination in reaching and locomotion. *Science*, 245(4923):1209–10, Sept. 1989. ISSN 0036-8075.

S. Glasauer, M.-A. Amorim, I. Viaud-Delmon, and A. Berthoz. Differential effects of labyrinthine dysfunction on distance and direction during blindfolded walking of a triangular path. *Exp Brain Res*, 145(4):489–97, Aug. 2002. ISSN 0014-4819.

R. Grasso, S. Glasauer, Y. Takei, and A. Berthoz. The predictive brain: anticipatory control of head direction for the steering of locomotion. *Neuroreport*, 7(6):1170–4, Apr. 1996. ISSN 0959-4965.

C. M. Harris and D. M. Wolpert. Signal-dependent noise determines motor planning. *Nature*, 394(6695):780–4, Aug. 1998. ISSN 0028-0836.

H. Hicheur, S. Glasauer, S. Vieilledent, and A. Berthoz. Head direction control during active locomotion in humans. In *Head Direction Cells and the Neural Mechanisms of Spatial Orientation.*, pages 383–408. MIT Press, Cambridge, MA, 2005a.

H. Hicheur, S. Vieilledent, M. J. E. Richardson, T. Flash, and A. Berthoz. Velocity and curvature in human locomotion along complex curved paths: a comparison with hand movements. *Exp Brain Res*, 162(2):145–54, Apr. 2005b. ISSN 0014-4819.

H. Hicheur, A. V. Terekhov, and A. Berthoz. Intersegmental coordination during human locomotion: does planar covariation of elevation angles reflect central constraints? *J Neurophysiol*, 96(3):1406–19, Sept. 2006. ISSN 0022-3077.

T. Imai, S. T. Moore, T. Raphan, and B. Cohen. Interaction of the body, head, and eyes during walking and turning. *Exp Brain Res*, 136(1):1–18, Jan. 2001. ISSN 0014-4819.

P. M. Kennedy, A. N. Carlsen, J. T. Inglis, R. Chow, I. M. Franks, and R. Chua. Relative contributions of visual and vestibular information on the trajectory of human gait. *Exp Brain Res*, 153(1):113–7, Nov. 2003. ISSN 0014-4819.

F. Lacquaniti, C. Terzuolo, and P. Viviani. The law relating the kinematic and figural aspects of drawing movements. *Acta Psychol (Amst)*, 54(1-3): 115–30, Oct. 1983. ISSN 0001-6918.

P. Morasso. Spatial control of arm movements. *Exp Brain Res*, 42(2):223–7, 1981. ISSN 0014-4819.

C. Papaxanthis, V. Dubost, and T. Pozzo. Similar planning strategies for whole-body and arm movements performed in the sagittal plane. *Neuroscience*, 117(4):779–83, 2003. ISSN 0306-4522.

A. E. Patla, S. D. Prentice, S. Rietdyk, F. Allard, and C. Martin. What guides the selection of alternate foot placement during locomotion in humans. *Exp Brain Res*, 128(4):441–50, Oct. 1999. ISSN 0014-4819.

Q.-C. Pham, H. Hicheur, G. Arechavaleta, J.-P. Laumond, and A. Berthoz. The formation of trajectories during goal-oriented locomotion in humans. ii. a maximum smoothness model. *Eur J Neurosci*, 26(8):2391–403, Oct. 2007. ISSN 0953-816X.

T. Pozzo, A. Berthoz, and L. Lefort. Head stabilization during various locomotor tasks in humans. i. normal subjects. *Exp Brain Res*, 82(1):97–106, 1990. ISSN 0014-4819.

P. Prévost, Y. Ivanenko, R. Grasso, and A. Berthoz. Spatial invariance in anticipatory orienting behaviour during human navigation. *Neurosci Lett*, 339(3):243–7, Mar. 2003. ISSN 0304-3940.

M. J. E. Richardson and T. Flash. Comparing smooth arm movements with the two-thirds power law and the related segmented-control hypothesis. *J Neurosci*, 22(18):8201–11, Sept. 2002. ISSN 1529-2401.

J. F. Soechting and M. Flanders. Moving in three-dimensional space: frames of reference, vectors, and coordinate systems. *Annu Rev Neurosci*, 15: 167–91, 1992. ISSN 0147-006X.

E. Todorov. Optimality principles in sensorimotor control. *Nat Neurosci*, 7 (9):907–15, Sept. 2004. ISSN 1097-6256.

P. Viviani and M. Cenzato. Segmentation and coupling in complex movements. *J Exp Psychol Hum Percept Perform*, 11(6):828–45, Dec. 1985. ISSN 0096-1523.

W. H. Warren, B. A. Kay, W. D. Zosh, A. P. Duchon, and S. Sahuc. Optic flow is used to control human walking. *Nat Neurosci*, 4(2):213–6, Feb. 2001. ISSN 1097-6256.

R. M. Wilkie and J. P. Wann. Judgments of path, not heading, guide locomotion. *J Exp Psychol Hum Percept Perform*, 32(1):88–96, Feb. 2006. ISSN 0096-1523.

D. M. Wolpert. Computational approaches to motor control. *Trends Cogn Sci*, 1:207–216, 1997.