RESEARCH ARTICLE

Invariance of locomotor trajectories across visual and gait direction conditions

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Abstract We studied the influence of vision (walking with or without vision) and of gait direction (walking forward or backward) on goal-oriented locomotion in humans. Subjects had to walk, in a free environment, from a given position and orientation towards a distant arrow which constrained their final position and orientation. We found that the average trajectories were mostly similar across the tested conditions, which suggests that locomotor trajectories are generated at a high cognitive level and, to some extent, independently of the detailed sensory and motor implementation levels. The variability profiles around the average trajectories were similar across the gait direction conditions but differed greatly across the visual conditions, indicating the existence of motor-independent and vision-dependent control mechanisms. Taken together, our observations argue further in favour of a top-down implementation of goal-oriented locomotion, where the control of locomotion is specified at the level of whole-body trajectories and then implemented through specific motor strategies.

Keywords Human locomotion · Vision · Backward walking · Invariance · Locomotor trajectories

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Abbreviations
CNS   Central nervous system
VF   Vision forward
NF   No-vision forward
VB   Vision backward
NB   No-vision backward
TD   Trajectory deviation
MTD   Maximum trajectory deviation
VD   Velocity deviation
TS   Trajectory separation
MTS   Maximum trajectory separation
TL   Trajectory length

Introduction

Locomotion in humans is a complex motor and cognitive activity requiring multiple levels of control: from the production of repetitive coordination patterns of the legs to the adjustments of upper-body segments ensuring dynamic stability and to the formation of whole-body trajectories in space. These different levels are integrated together by the central nervous system (CNS) for the production and the regulation of the locomotor commands, allowing navigating efficiently in a particular environment. In this respect, a comprehensive understanding of locomotion requires investigating the *relations* between these different levels. Here, we set out to address the following question: How does a change in the conditions of production of the stepping patterns and/or a change in the visual conditions affect the formation of whole-body trajectories? Answering this question will allow further investigating the hypothesis that locomotor trajectories are planned and controlled at a

high cognitive level (Hicheur et al. 2007, Pham et al. 2007, Pham and Hicheur 2009).

Influence of gait direction and vision on the formation of locomotor trajectories

Influence of gait direction

We recently showed, in a simple goal-oriented task during which human subjects had to walk towards and throughout a doorway, that locomotor trajectories were stereotyped, which contrasted with a significantly greater variability in feet placements (Hicheur et al. 2007). This suggested that goal-oriented locomotion is planned and controlled at the level of whole-body trajectories rather than at the level of the steps. Recent brain imaging studies also revealed that structures such as the hippocampus, whose role in *navigation* is well known, are involved in imagined locomotion (Jahn et al. 2004). However, how dramatic changes in the walking conditions, such as the reversal of gait direction (walking backward), affect the formation of trajectories remains unknown. At the step-level, despite the complete reorganization of the muscular activation patterns that backward walking implies, the lower limbs *kinematics* were shown to be similar to those of forward walking after a reversal of the time axis (Thorstensson 1986, Grasso et al. 1998a). Whether this invariance also holds at the level of whole-body trajectories is one of the questions addressed by the present study.

Influence of vision

The crucial influence of vision on the formation of locomotor trajectories has been investigated through visually perturbed and nonvisual experimental protocols. Using prisms or virtual environments, researchers studied whether the perceived location of the target (Rushton et al. 1998), optic flow (Lappe et al. 1999) or a combination thereof (Warren et al. 2001) underlie the perception of self-motion and locomotion towards a distant target when visual feedbacks are available.

When no visual feedbacks are available, it was reported that subjects are still able to walk towards a previously seen distant target placed up to ~10 metres in front of them (Thomson 1983, see Loomis et al. 1992 for a review). Similarly, either during triangle completion (Loomis et al. 1993) or circular 'blind' locomotion experiments (Takei et al. 1997), changes in *orientation* were shown to be rather well implemented in nonvisual locomotion. In a recent study, we showed that subjects were able to combine the distance and orientation processing capabilities mentioned above to nonvisually walk with good precision towards a distant target defined in position

and orientation. Moreover, we remarked that subjects produced similar *average* trajectories in visual and nonvisual forward locomotion; in particular, the separation between the visual and the nonvisual average trajectories was found to be smaller than the variability within the visual trajectories (Pham and Hicheur 2009). This supports the hypothesis that a common *open-loop*, vision-independent process governs the formation of locomotor trajectories. Going a step further, by examining the *variability* around the average trajectories, we showed that similar *online* control mechanisms, likely based on optimal feedback control principles (Todorov and Jordan 2002), underlie visual and nonvisual forward locomotion (Pham and Hicheur 2009). However, whether similar results hold for nonvisual backward locomotion is still unknown, and the answer to this question may provide further insights into the control of nonvisual locomotion.

In order to understand the separate and combined effects of gait direction and of vision on locomotor trajectories, we designed an experimental protocol where subjects had to walk forward or backward, with or without vision. The comparison of locomotor trajectories across these different conditions allowed us to further explore the hypothesis that locomotor trajectories are planned and controlled at a high cognitive level and, to some extent, independently of the detailed sensorimotor implementations (this notion has already been proposed and verified in hand movements, see e.g. Morasso 1981, Atkeson and Hollerbach 1985).

Methods

In this study, we wanted to study the effects of vision [walking with (V) or without (N) vision] and of gait direction [walking forward (F) or backward (B)] on locomotor trajectories and on the steering behaviour. We used a 2×2 design, implying four experimental conditions: walking with vision forward (VF), with vision backward (VB), without vision forward (NF) and without vision backward (NB). The data corresponding to the forward walking conditions VF and NF had been partly presented by Pham and Hicheur (2009). They were re-analysed here for the comparisons of VF vs. VB, NF vs. NB and VB vs. NB. The data corresponding to the backward walking conditions VB and NB have not been presented elsewhere.

Experimental methods

Subjects and materials

Fourteen healthy male subjects volunteered for participation in the experiment. The experiment conformed to the Code of Ethics of the Declaration of Helsinki, and all

procedures were carried out with the adequate understanding and written consent of the subjects. The mean age, height and weight of the subjects were respectively equal to 24.6 ± 3.2 years, 1.80 ± 0.04 m and 73.3 ± 5.7 kg.

The 3D positions of two light-reflective markers were used in the analysis. The markers' positions were recorded using an optoelectronic Vicon V8 motion capture system wired to 12 cameras with a 120-Hz sampling frequency. To study whole-body trajectories 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. 2007).

The dimensions of the laboratory where the experiments took place were approximately 10 m × 10 m × 5 m (length, width and height, respectively).

Protocol

In each trial, the subject had to start from a fixed position in the laboratory and walk towards a distant, oriented target, indicated by a cardboard arrow of dimension 1.20 m × 0.25 m.

We constrained the subject's initial travelling direction by asking him to start at the position whose coordinates were (0,–1 m) in the laboratory (X, Y) reference frame and to walk the first metre [from (0,–1 m) to (0, 0)] orthogonally to the X-axis. We imposed the subject's final travelling direction by asking the subject to enter the arrow by the shaft and to stop walking above the arrow head (Fig. 1a, b). No other restriction relative to the path to follow was provided to the subject between the initial and final positions.

The shaft of the arrow could be placed in 7 possible positions (numbered 1–7), at distances from the position (0, 0) ranging from 2 m (position 1) to 5.7 m (position 5), and the arrow could be oriented in 4 possible directions (labelled N, E, W and S), resulting in 19 possible configurations. Figure 1b depicts 11 of these configurations, omitting the 8 configurations corresponding to positions 6 and 7, which were symmetrical to the 8 configurations corresponding to positions 4 and 5, respectively.

The three configurations (or targets) 1N, 2N and 3N were located in front of the subject. These targets were termed 'straight targets' since the trajectories corresponding to these targets were approximately straight. Eight configurations (4N, 4E, 4W, 4S, 5N, 5E, 5W and 5S: right 'angled targets') were located on the subject's right, and 8 configurations (6N, 6E, 6W, 6S, 7N, 7E, 7W and 7S: left 'angled targets') were located on the subject's left; the latter targets were symmetrical to the former with respect to the Y-axis.

The three straight targets were used for all 14 subjects. The right 'angled targets' were used for a subgroup of 6 subjects, and the left 'angled targets' were used for the remaining 8 subjects. Thus, each subject generated 132 trajectories corresponding to 11 spatial targets (3 straight + 8 angled) × 4 conditions × 3 trials, so that a total of 1848 trajectories (14 subjects × 132 trials) were recorded for this experiment. Incorrectly captured trials were discarded, resulting in 1608 trajectories being actually processed.

The subject walked at his preferred, self-selected speed either with eyes open (visual conditions: VF, VB) or closed (nonvisual conditions: NF, NB). In the visual conditions, the arrow was visible throughout the whole movement. In the nonvisual conditions, the subject first observed the arrow while standing at the starting position. When the subject was ready, he closed his eyes and attempted to complete the task—walk the first metre orthogonally to the
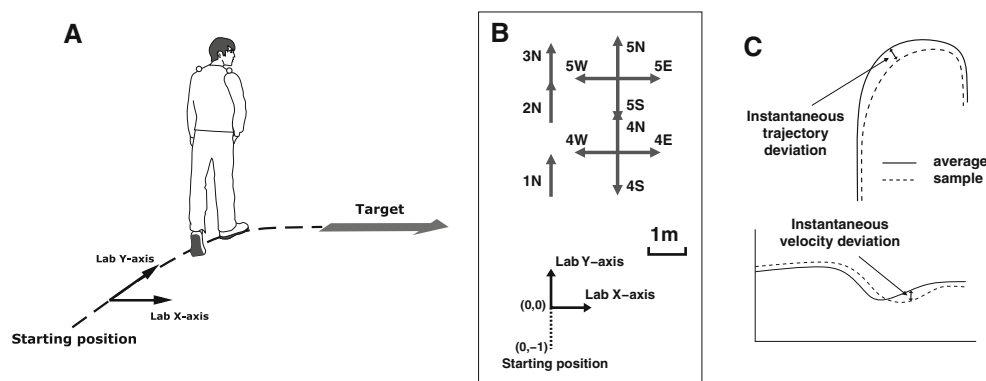

Fig. 1 **a** Experimental protocol: subjects had to start from a fixed position in the laboratory and walk towards a distant arrow placed on the ground. Subjects had to enter the *arrow* by the shaft and stop above the *arrow head*. **b** Spatial disposition of the 19 targets: each target was referred to by a number (1–7) indicating the position and by a letter [N (north), S (south), E (east) and W (west)] indicating the orientation. **c** Instantaneous trajectory deviation [TD(t)] and instantaneous velocity deviation [VD(t)], which measure respectively the variability of actual trajectories around the average trajectory and the variability of actual velocity profiles around the average velocity profile. **d** Definition of the head and trunk angles

X-axis, enter the arrow by the shaft and stop above the arrow head—without vision. The experimenter removed the arrow right after the observation period (which typically lasted less than 3 s) in order to avoid tactile feedbacks. Once the subject had completely stopped, he was asked to keep his eyes closed. The experimenter then took the subject's hand and guided him randomly for a few seconds in the laboratory before stopping at a random position. The subject was then allowed to re-open his eyes and to go back to the starting position. This procedure prevented the subject from post-execution spatial calibration using kinaesthetic cues.

At the beginning of the backward walking trials, the subject stood at position (0, −1 m) with his back facing the experimental field. He was then asked to walk backward towards the target. No restriction was imposed on the subject's head movements, so that he was free to turn his head to visualize the target's position at the beginning of the trial (in conditions VB and NB), and to visually track the target's position during the whole trial (in condition VB).

The trials were randomized in order to avoid learning effects for a particular condition or target. The subject completed two to three trials before the experiment actually started in order to be familiar with the task and to dispel any fear of hitting the walls during the nonvisual trials (the distance between the most distant target and the wall was ∼3 m).

Analysis of the locomotor trajectories

All the data analyses below were performed with the free software GNU Octave, unless otherwise stated.

The beginning ($t = 0$) of each trajectory was set to the time instant when the subject crossed the X-axis. In order to have the same criterion for the visual and nonvisual conditions, the end of each trajectory ($t = 1$, after time-rescaling, which allowed comparing trajectories with different durations, see Pham et al. 2007) was set to the time instant when the subject's speed became smaller than 0.06 m s^{-1} (this value was smaller than 5% of the average nominal walking speed). We chose this strictly positive threshold because even when the subject had completely stopped, the speed of their shoulders' midpoint was not exactly zero due to the small residual movements of the upper body. The average length across targets and subjects of the trajectories as so defined was 5.6 m in condition VF.

When a derivative of the position (velocity, acceleration, etc.) was needed, a second-order Butterworth filter with cut-off frequency 6.25 Hz was applied before the derivation.

The average trajectories ($x_{av}(t)$, $y_{av}(t)$), the instantaneous trajectory deviation (TD) at time t, the maximum trajectory

deviation (MTD), the instantaneous velocity deviation (VD) and the maximum velocity deviation (MVD) were computed as in Pham et al. (2007), to which the reader is referred for more details.

Comparison of trajectories in two conditions

In order to compare the average trajectories recorded in two different conditions A and B, we defined for each target the instantaneous trajectory separation (TS) as

$$TS_{A/B}(t) = \sqrt{(x_A(t) - x_B(t))^2 + (y_A(t) - y_B(t))^2} \quad (1)$$

where (x_A, y_A) and (x_B, y_B) denote the average trajectories, respectively, in condition A and in condition B.

We then defined the maximum trajectory separation (MTS) as

$$MTS_{A/B} = \max_{0 \le t \le 1} TS_{A/B}(t). \quad (2)$$

Results

Targets pooling

Six subjects walked towards targets located on their left, and eight subjects walked towards targets located on their right (see Fig. 1b). We found no significant effect of the side on the parameters of interest: for instance, the $MTS_{L/R}$ (MTS between the average trajectory of the left trajectories and that of the right trajectories) was smaller than the MTD_R (MTD of the right trajectories) in the four conditions VF, NF, VB and NB (on average across targets and conditions, $MTS_{L/R} = 0.29$ m while $MTD_R = 0.54$ m). In the two-way ANOVA test with replications where the factors were the measure ($MTS_{L/R}$ versus MTD_R) and the conditions (VF, NF, VB and NB), the effect of the measure was significant [$F(3,80) = 44.8$, $P < 0.05$].

Consequently, for all the following analyses, we flipped the left trajectories towards the right and pooled them together with their symmetrical trajectories (trajectories of target 4 with those of target 6 and trajectories of target 5 with those of target 7).

Effects of vision

Comparison of visual backward (VB) and nonvisual backward (NB) conditions

In condition VB, since no restrictions were imposed on head movements, the subjects tended to turn their head backwards in order to keep track of the target and to monitor their own positions and orientations in space. We observed that the average trajectories in conditions VB and

NB were very similar, albeit to a lesser extent than in the comparison of conditions VF and NF (cf. Pham and Hicheur 2009, in particular Fig. 3 of that reference). This observation was verified here both at the path level (Fig. 2A1, 2B1, 2C1) and at the normalized velocity profile level (Fig. 2A2, 2B2, 2C2). Note, however, that the average absolute velocity was smaller in condition NB than in VB (respectively 0.79 m.s^{-1} and 0.88 m.s^{-1} across trials and targets).

Quantitatively, the average maximal trajectory separation $MTS_{VB/NB}$ across the 11 tested targets were 0.50 m (Fig. 2d) in absolute terms, or 9.2% of the VB trajectory length (TL). These values are to be compared with the average MTD_{VB}–maximum trajectory deviation within condition VB (which was 0.38 m or 6.4% of the VB TL) and with the average MTD_{NB} (which was 0.90 m or 15.7% of the NB TL). In other words, the separation between the average trajectory of VB and that of NB was much smaller than the variability of the trajectories within NB, and not much larger than the variability within VB.

Regarding the variability profiles, we observed large differences between conditions VB and NB, in terms of both magnitude ($MTD_{VB} = 0.38$ m, which was much smaller than $MTD_{NB} = 0.90$ m) and shapes: in condition VB, the variability decreased towards 0 at the end of the movement, yielding bump-shape profiles, while in condition NB, the variability never reached 0 at the end of the movement (Fig. 2A3, 2B3, 2C3, see also the comparison of NF/NB variability profiles below).

Effects of gait direction

Comparison of visual forward (VF) and visual backward (VB) conditions

In targets which imposed no change in curvature sign (or equivalently whose paths did not contain an inflection point, i.e. all targets except 4W, 4N, 5W and 5N), the average trajectories observed in conditions VF and VB were very similar at the path level (targets 4E and 5S,
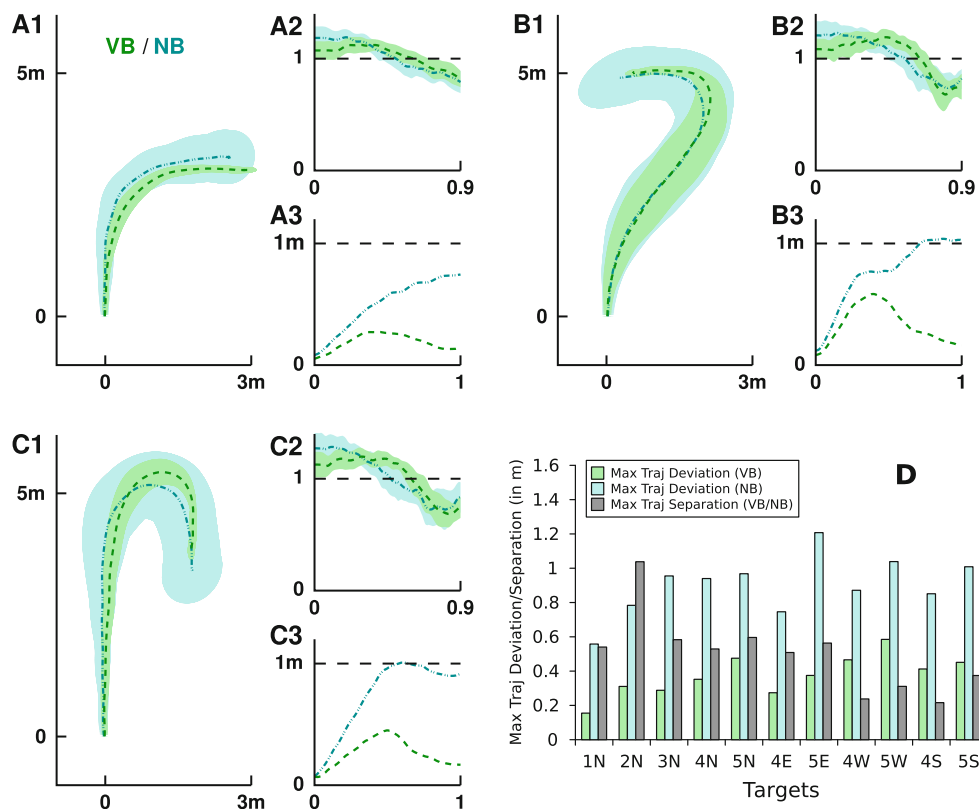

Fig. 2 Comparison of locomotor trajectories in the visual backward (VB: *green*, *dashed lines*) and nonvisual backward (NB: *cyan*, *dotted-dashed lines*) conditions. **a** Comparisons for target 4E. *A1* geometric paths of the average trajectories. We also plotted the variance ellipses around the average trajectory at every time instant (see "Methods") in light green and light cyan. *A2* average velocity profiles. The velocity profiles were normalized so that their average values over the movement duration equals 1 (see "Methods"). Standard deviations around the average velocity profiles are in light green and light cyan. *A3* trajectory variability profiles [TD(t)]. **b** Same as in **a**, but for target 5W. **c** Same as in **a**, but for target 5S. **d** maximal trajectory deviation/separation (MTD/MTS) in metres: MTD in condition VB (*green bars*), MTD in condition NB (*cyan bars*) and MTS between the average trajectory of VB and NB (*grey bars*)

Fig. 3A1, 3C1). In targets which imposed a change in curvature sign (4W, 4N, 5W and 5N), the VB paths were slightly shifted to the interior of the main curve with respect to the VF paths (targets 5W: Fig. 3B1; also target 4W: not shown). However, quantitatively, this difference resulted in a MTS$_{VF/VB}$ smaller than 0.4 m (Fig. 3D). In terms of the normalized velocity profiles, we found very similar patterns, in every target (Fig. 3A2, 3B2, 3C2). Note however that, as above, the average absolute velocity was smaller in condition VB than in VF (respectively 0.88 m.s^{-1} and 1.05 m.s^{-1} across trials and targets).

Quantitatively, the average MTS$_{VF/VB}$ across the 11 tested targets were 0.22 m (Fig. 3d) in absolute terms, or 4.0% of the VF TL. These values are to be compared with the average MTD$_{VF}$ (which was 0.31 m or 5.7% of the VF TL) and with the average MTD$_{VB}$ (which was 0.38 m or 6.4% of the VB TL). In other words, the separation between the average trajectory of VF and that of VB was smaller than the variabilities of the trajectories within each condition.

Finally, we noted that the variability profiles were similar in the two conditions, in terms of both magnitudes (average MTD$_{VF}$ = 0.31 m and average MTD$_{VB}$ = 0.38 m) and shapes (Fig. 3A3, 3B3, 3C3).

Comparison of nonvisual forward (NF) and nonvisual backward (NB) conditions

Here, the similarity of the average trajectories was not as strong as in the previous comparison. Yet, it was still remarkable given the difficulty of the task (walking to distant targets defined in both position and orientation without visual feedback). At the path level, the average trajectories globally displayed the same forms, with some shift between the two conditions (Fig. 4A1, 4B1, 4C1). In particular, in targets which imposed a change in curvature sign, we observed that, as in the VF/VB comparison, the NB paths were shifted towards the interior of the main curve with respect to the NF paths (target 5 W: Fig. 4B; also target 4 W: not shown). As in the VF/VB comparison, the normalized velocity profiles were very similar in the two compared conditions, in all targets (Fig. 4A2, 4B2, 5C2). Note however that, as above, the average absolute velocity was smaller in condition NB than in NF (respectively 0.79 m.s^{-1} and 0.89 m.s^{-1} across trials and targets).

Quantitatively, the average MTS$_{NF/NB}$ across the 11 tested targets were 0.38 m (Fig. 4d) in absolute terms, or 6.9% of the NF trajectory length. These values are to be compared with the average MTD$_{NF}$ (which was 0.74 m or
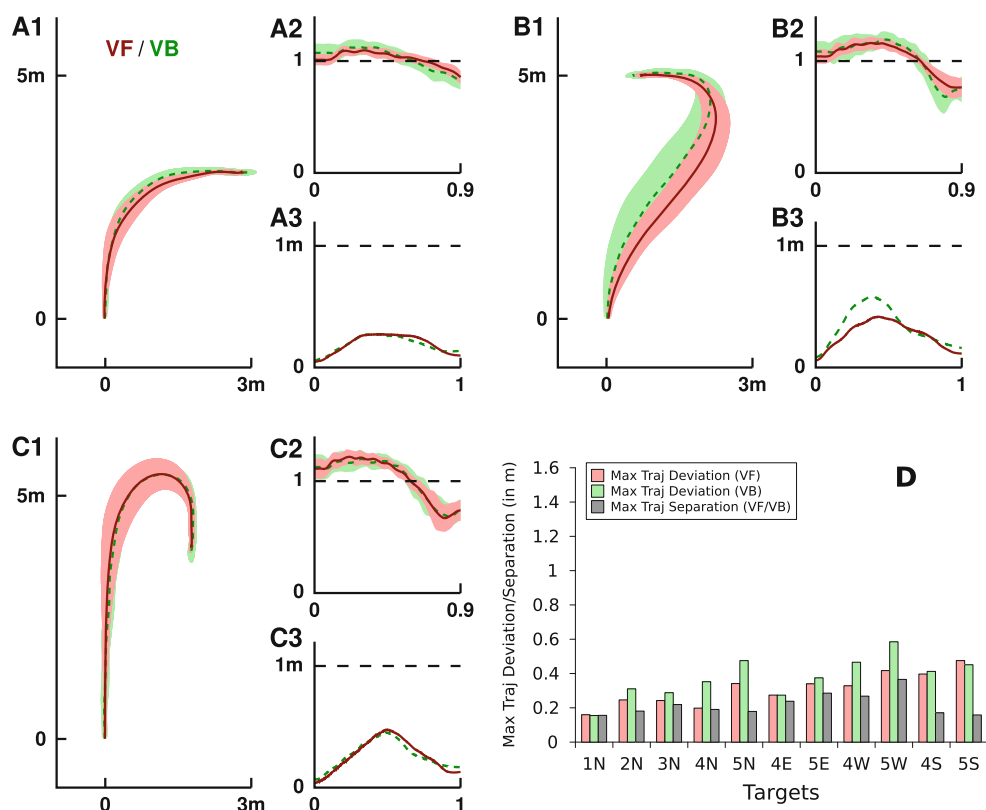

Fig. 3 Comparison of locomotor trajectories in the visual forward (VF: *red*, *plain lines*) and visual backward (VB: *green*, *dashed lines*) conditions. For details, see legend of Fig. 2
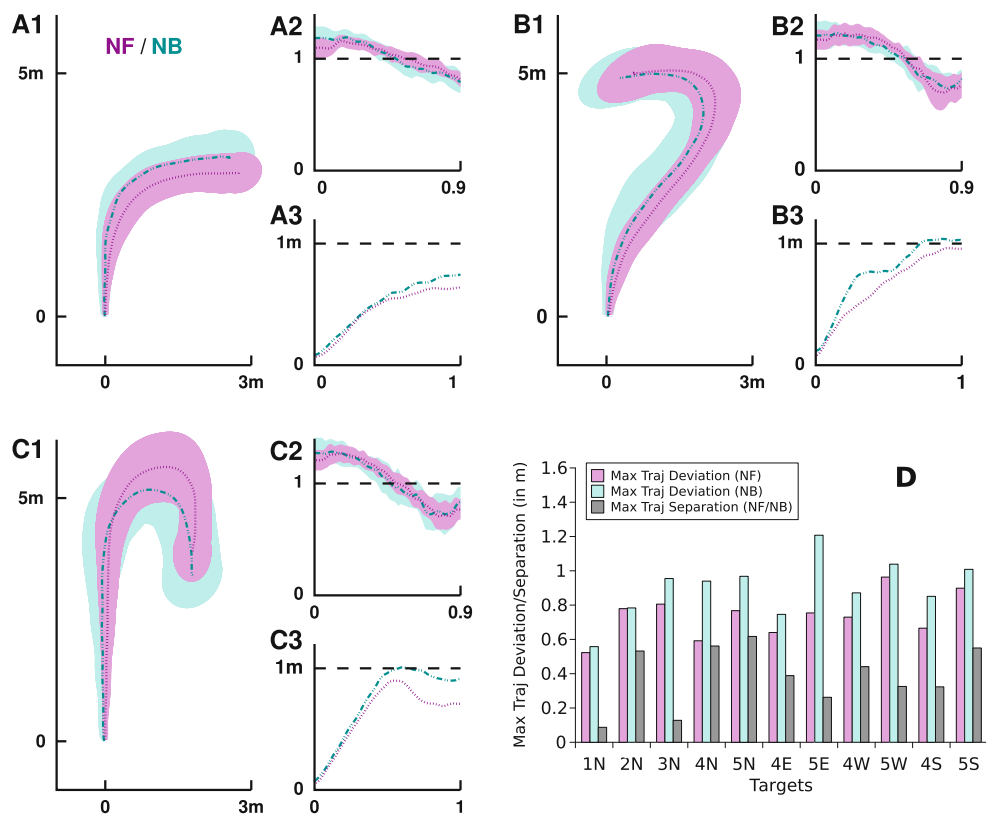
Fig. 4 Comparison of locomotor trajectories in the nonvisual forward (NF: *magenta*, *dotted lines*) and nonvisual backward (NB: *cyan*, *dotted-dashed lines*) conditions. For details, see legend of Fig. 2

13.6% of the NF TL) and with the average MTD_{NB} (which was 0.90 m or 16.5% of the NB TL). In other words, the separation between the average trajectory of NF and that of NB was much smaller than the variabilities of the trajectories within each condition.

In terms of the variability profiles, we observed a larger variability in condition NB (see the values of MTD given above). However, the difference between conditions NF and NB was low as compared with the VF/NF and VB/NB comparisons. In addition, the variability profiles displayed similar shapes in the two conditions NF and NB (Fig. 4A3, 4B3, 4C3). In particular, as in condition NF, the variability profile of NB was *nonmonotonic* in some angled targets: cf. target 5S in Fig. 4C3. This feature, first reported by Pham and Hicheur (2009) for condition NF, is particularly remarkable since, in absence of visual feedback, one would expect a monotonically increasing variability profile (see "Discussion" for more details).

Discussion

We experimentally examined the properties of locomotor trajectories and of the steering behaviour performed under different visual (walking with or without vision) and motor

(walking forward or backward) conditions. Qualitatively, we observed that the *average trajectories* were highly similar across the visual and the gait direction conditions (the differences of the average trajectories across conditions were comparable—and inferior in most cases—to the variabilities within a single condition). This similarity held at both the geometric level (the paths) and the kinematic level (the normalized velocity profiles), despite differences across conditions in the *absolute* walking speeds. On the other hand, the *variability profiles* were found to differ across the visual conditions but not across the gait direction conditions.

Open-loop and online control mechanisms in the formation of whole-body trajectories in visual and nonvisual locomotion

We reported in a previous work that the absence of vision did not affect the average trajectories during goal-oriented *forward* locomotion (comparison of VF versus NF locomotion in Pham and Hicheur 2009). We find here that this observation also holds in the context of *backward* locomotion, as shown above by comparing VB and NB.

Between conditions VF and VB also, the visual input patterns differed greatly. In condition VB, the subjects

tended to turn their head backwards and towards the interior of the curve in order to keep track of the target and to monitor their own positions and orientations in space (note that Grasso et al. 1998b reported a different behaviour: in their experimental set-up, where the subjects had simply to walk around a 3-m-legged 90° corner with no spatial constraints on the final position, the authors observed a deviation of the head towards the *exterior* of the curve in condition VB). In any case, the head orientation profiles we recorded were drastically different between conditions VF and VB (a difference larger than 120°), which affected both the incoming optic flow and the perceived direction of the target with respect to the body (Rushton et al. 1998, Warren et al. 2001). Despite these important differences, we still observed a striking similarity of both the average trajectories and the variability profiles between conditions VF and VB.

We proposed previously a general architecture for the control of locomotor trajectories (Pham and Hicheur 2009), with a) an open-loop component—which is reflected in the average trajectories—and b) an online feedback control model—which is reflected in the variability profiles. From this perspective, our observation of similar average trajectories in visual and nonvisual backward locomotion supports the hypothesis that there exist *vision*-independent open-loop processes in the production of locomotor trajectories.

Regarding the *online* control mechanisms, we observed that the variability profiles in conditions NF and NB were also rather similar, in both magnitude and shape (Fig. 4). In Pham and Hicheur (2009), we interpreted the *nonmonotonic* profiles observed in condition NF as reflecting the existence of online control mechanisms even in absence of vision. We decomposed this profile as the sum of (i) a *bump-shape profile*, which is already present in condition VF and which presumably results from the interplay between execution noise and optimal feedback control [in condition VF, this bump shape can be explained as follows: at $t = 0$ and $t = 1$, the variability is close to 0 since the initial and final positions are fixed. In between, execution noise makes actual trajectories deviate from the average trajectory. An optimal feedback controller would correct only the deviations that interfere with the task (i.e. reaching the desired final position at $t = 1$); those that are not corrected by the controller would then accumulate and give rise to a bump around the middle of the variability profile (Pham and Hicheur 2009)] and of (ii) a *linearly increasing profile*, which is related to the state estimation errors caused by the absence of visual feedbacks. Here, the variability profiles observed in angled targets in condition NB were also nonmonotonic and bear important resemblances with the profiles observed in condition NF. This suggests that the two-source decomposition mentioned above may also hold, at least qualitatively, for nonvisual *backward*

locomotion, strengthening thereby the hypothesis that optimal feedback control underlies nonvisual locomotion (i.e. that, in nonvisual locomotion, the subjects make optimal online feedbacks towards an *estimated* position of the target) in general.

Motor independence of trajectory formation

How locomotor trajectories are affected by a severe reorganization of the walking patterns was investigated here. Despite the differences between stepping motor patterns at the leg level during forward and backward walking (in addition to the perceptual level previously discussed), both the observed *average trajectories and the variability profiles* were strikingly similar in conditions VF and VB, suggesting similar open-loop and online control mechanisms in the production of whole-body trajectories in these two conditions. This further strengthens the hypothesis that the CNS plans and controls goal-oriented locomotion at the level of whole-body trajectories in space and, to some extent, independently of the motor implementation level. Then, a detailed motor strategy (in terms of foot placements, muscular activations, intersegmental coordination, etc.) would be produced to actually *implement* these trajectories. This can be related to the classical observation that arm movements are planned at the level of hand trajectory in space (see e.g. Morasso 1981, Atkeson and Hollerbach 1985) or, more recently, to the results of Steck and colleagues (2009), who showed that the estimation of homing distance in desert ants is preserved despite severe disturbance of walking behaviour following limb loss.

We noted, however, some limitations to our experimental findings. For targets 4W and 5W which impose inflection points in the trajectories, the differences between the average trajectories in the VF and VB conditions were higher than for the other targets (see "Results"). Since the existence of inflection points may dramatically increase the complexity of the task, bio-mechanical differences may play a greater role in shaping the trajectories. In the same vein, it could be noted that, in highly constrained tasks (such as avoidance tasks: Patla et al. 1999), the foot placement may become stereotyped and precisely monitored by the CNS, which contrasts with the highly variable foot placement patterns observed in free-environment experiments (Hicheur et al. 2007).

In conclusion, our observations argue in favour of the hypothesis that the open-loop component in the control of whole-body trajectories is mostly independent of the detailed sensory and motor implementation. Such a control could in turn be based on the maximization of trajectory smoothness (Pham et al. 2007, Pham and Hicheur 2009) or on *geometrical invariance* principles (for instance Bennequin et al. 2009 showed that the locomotor speed along

complex trajectories obeys a mixture of Euclidian, equi-affine and affine invariances).

References

Atkeson CG, Hollerbach JM (1985) Kinematic features of unrestrained vertical arm movements. J Neurosci 5:2318–2330

Bennequin D, Fuchs R, Berthoz A, Flash T (2009) Movement timing and invariance arise from several geometries. PLoS Comput Biol 5:e1000426. doi:10.1371/journal.pcbi.1000426

Grasso R, Bianchi L, Lacquaniti F (1998a) Motor patterns for human gait: backward versus forward locomotion. J Neurophysiol 80:1868–1885

Grasso R, Prévost P, Ivanenko YP, Berthoz A (1998b) Eye-head coordination for the steering of locomotion in humans: an anticipatory synergy. Neurosci Lett 253:115–118

Hicheur H, Pham QC, Arechavaleta G, Laumond JP, Berthoz A (2007) The formation of trajectories during goal-oriented locomotion in humans. I. A stereotyped behaviour. Eur J Neurosci 26:2376–2390

Jahn K, Deutschländer A, Stephan T, Strupp M, Wiesmann M, Brandt T (2004) Brain activation patterns during imagined stance and locomotion in functional magnetic resonance imaging. Neuroimage 22:1722–1731

Lappe M, Bremmer F, van den Berg AV (1999) Perception of self-motion from visual flow. Trends Cogn Sci 3:329–336

Loomis JM, Da Silva JA, Fujita N, Fukusima SS (1992) Visual space perception and visually directed action. J Exp Psychol Hum Percept Perform 18:906–921

Loomis JM, Klatzky RL, Golledge RG, Cicinelli JG, Pellegrino JW, Fry PA (1993) Nonvisual navigation by blind and sighted: assessment of path integration ability. J Exp Psychol Gen 122:73–91

Morasso P (1981) Spatial control of arm movements. Exp Brain Res 42:223–227

Patla AE, Prentice SD, Rietdyk S, Allard F, Martin C (1999) What guides the selection of alternate foot placement during locomotion in humans. Exp Brain Res 128:441–450

Pham QC, Hicheur H (2009) On the open-loop and feedback processes that underlie the formation of trajectories during visual and nonvisual locomotion in humans. J Neurophysiol 102:2800–2815

Pham QC, Hicheur H, Arechavaleta G, Laumond JP, Berthoz A (2007) The formation of trajectories during goal-oriented locomotion in humans. II. A maximum smoothness model. Eur J Neurosci 26:2391–2403

Rushton SK, Harris JM, Lloyd MR, Wann JP (1998) Guidance of locomotion on foot uses perceived target location rather than optic flow. Curr Biol 8:1191–1194

Steck K, Wittlinger M, Wolf H (2009) Estimation of homing distance in desert ants, Cataglyphis fortis, remains unaffected by disturbance of walking behaviour. J Exp Biol 212:2893–2901

Takei Y, Grasso R, Amorim MA, Berthoz A (1997) Circular trajectory formation during blind locomotion: a test for path integration and motor memory. Exp Brain Res 115:361–368

Thomson JA (1983) Is continuous visual monitoring necessary in visually guided locomotion? J Exp Psychol Hum Percept Perform 9:427–443

Thorstensson A (1986) How is the normal locomotor program modified to produce backward walking? Exp Brain Res 61:664–668

Todorov E, Jordan MI (2002) Optimal feedback control as a theory of motor coordination. Nat Neurosci 5:1226–1235

Warren WH Jr, Kay BA, Zosh WD, Duchon AP, Sahuc S (2001) Optic flow is used to control human walking. Nat Neurosci 4:213–216