

## Eye-head coordination for the steering of locomotion in humans: an anticipatory synergy

Renato Grasso<sup>a,\*</sup>, Pascal Prévost<sup>b</sup>, Yuri P. Ivanenko<sup>a,c</sup>, Alain Berthoz<sup>b</sup>

<sup>a</sup>*Section of Human Physiology, Scientific Institute S. Lucia, 00179 Rome, Italy*

<sup>b</sup>*LPPA, Collège de France, Paris, 75005, France*

<sup>c</sup>*Institute for Information Transmission Problems, Russian Academy of Science, Moscow, 101447, Russia*

Received 6 July 1998; received in revised form 27 July 1998; accepted 27 July 1998

---

### Abstract

We investigated head and gaze orientation in six healthy volunteers walking along 90° corner trajectories, both at light and with eyes closed. We found that head and eyes systematically deviated toward the future direction of the curved trajectory. Anticipation lead was about 1 s. Strikingly, the same behaviour was observed in darkness. In backward (BW) locomotion along the trajectory (from end- to start-point), gaze deviated toward the opposite direction, such that the forward locomotor pattern did not appear time-reversed. Orienting movements displayed higher amplitude, reproducibility and time lead in the forward (FW) direction at light. We suggest that anticipatory orienting synergies belong to the behavioural repertoire of human navigation and may reflect the need to prepare a stable reference frame for intended action. © 1998 Elsevier Science Ireland Ltd. All rights reserved

**Keywords:** Locomotion; Steering; Head movements; Eye-head coordination; Anticipation; Feed-forward control

---

What happens to gaze orientation during human navigation? Is gaze anticipating the position of potential targets to be reached? If this is the case, what signals drive eye-head coordinated movements? In a previous work [7] we have found that head direction during circular walks is consistently directed toward the side of the trajectory concavity. Land and Lee [8] found that when we drive a car, we direct our gaze toward the inner side of the road bend we are about to take.

Here, we concentrate on locomotor turns around corners. Anticipatory head movements toward the direction to be walked have been shown to characterise this situation and to develop very early in childhood [5]. In the present study, we measured head and eye movements in subjects walking along the same 90° corner trajectory both at light and with

eyes closed and in FW and BW locomotion. Our aim was to extract invariant features peculiar to gaze orienting movements during locomotor navigation.

Six healthy volunteers (aged  $33 \pm 4$  years) participated in this study. The experimental paradigm was the following: subjects were asked to walk, at their preferred speed, around an obstacle (a 50 cm high and wide box) they could see from a given starting position and to reach a final position in another point of a richly textured environment. The initial and final positions of the subject and the position of the obstacle were selected so that the resulting trajectory was a 90°, 3 m legged corner. After performing at light (light FW), subjects repeated the experiment with eyes closed (dark FW). Then they had to walk backwards from the arrival back to the start point, first at light (light BW) then with eyes closed (dark BW). Steering was therefore to the right in FW trials and to the left for BW trials. Three trials per subject per condition were used for statistical analysis.

The ELITE [4] system computed (time resolution = 0.01 s) the instantaneous position of two head markers placed along the naso-occipital axis of a helmet wore by the sub-

---

\* Corresponding author. Fisiologia Neuromotoria, C.N.R., Istituto Scientifico S. Lucia, via Ardeatina 306, 00179 Roma, Italy.  
Tel.: +39 6 51501473; fax: +39 6 51501477;  
e-mail: rgrasso@giannutri.caspur.it

jects. The root mean square error for position was  $<1.5$  mm and the sampling volume was centred about the corner vertex. Instantaneous walking direction (i.e. the orientation of the tangent to head trajectory), head position (x,y coordinates), head orientation in space ( $\alpha$ ) and head orientation relative to trajectory direction ( $\theta$ ) were calculated as described in the previous study [7]). Signals were digitally low-pass filtered with a cut-off frequency of 5 Hz before undergoing further analysis. Eye movements were recorded by means of electro-oculography (EOG). Horizontal calibration was performed before and after the experiment. Zero position was checked and adjusted at the beginning of each trial.

We reasoned that if visual navigation was based on available visual information, anticipatory movements should disappear in darkness. However, because anticipatory movements may be embedded in and totally specified by the motor patterns for curvilinear locomotion, we tested also

the case of backward locomotion along the same trajectory (from arrival to start point). The prediction was that head and eye movements would be the time-reversed copy of those belonging to the forward case (i.e. they should be oriented toward the same side relative to the trajectory) had they been hardwired in a specific motor pattern [6], whereas they would be directed toward the opposite side if they were dependent on a true anticipation relative to the intended direction of motion.

The main methodological problem of this study was the assessment of the corner position for the comparison of light and dark trials. The position could be selected on the basis of the kinematic or geometric properties of the trajectory generated by the subject [5]. We screened different criteria based on quantitative locomotor parameters (instantaneous head linear and angular speed) and a geometric parameter (trajectory curvature) and eventually selected as the subjective corner position, the position where local curvature (the

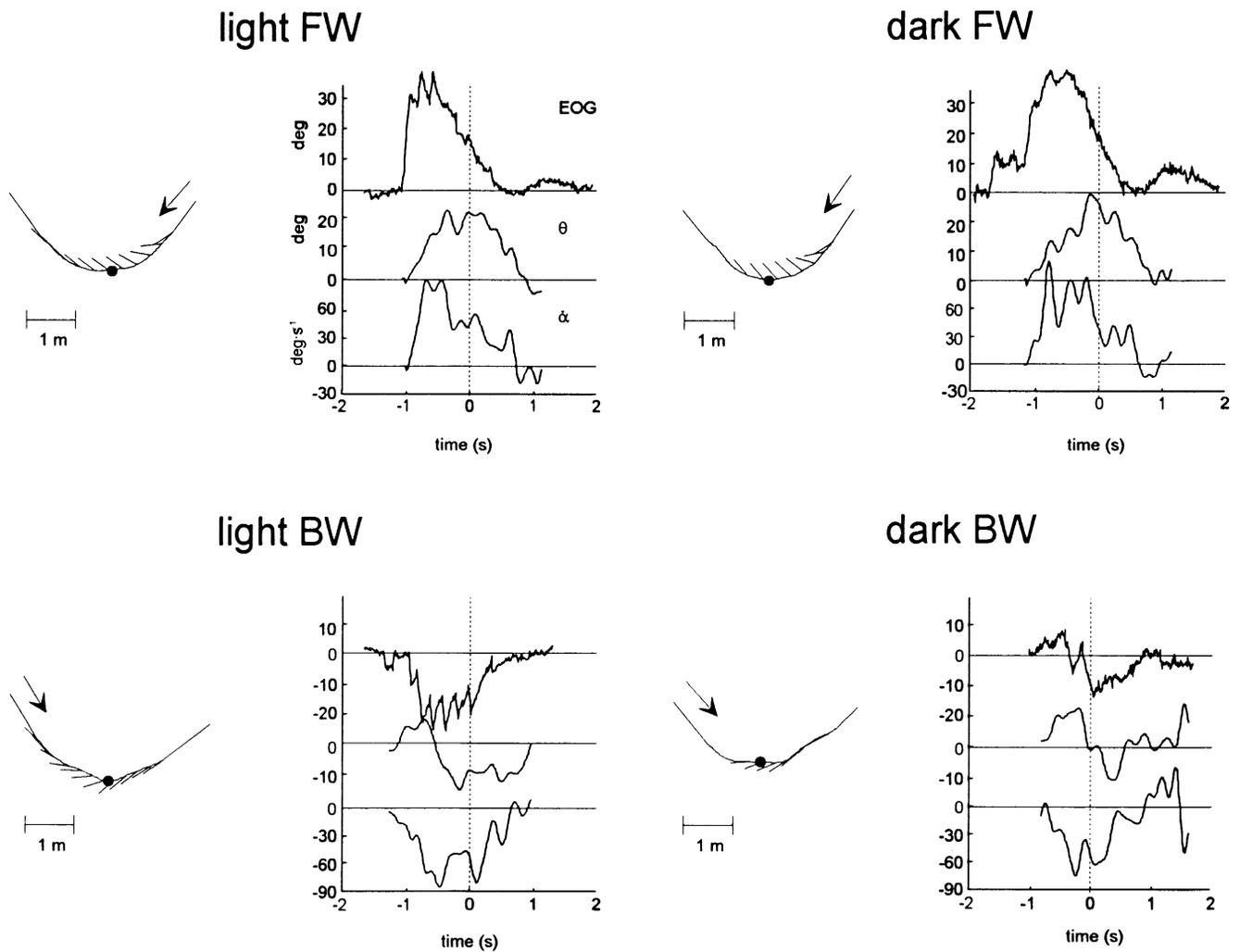


Fig. 1. Sample case: one trial for each experimental condition is shown. Gaze direction (eyes-in-head plus head-on-trajectory) is represented by sticks superimposed to the trajectory drawn by the head midpoint (left panels). The filled dark circle represents the subjective corner position (see methods). The time course of horizontal EOG, of the head direction relative to the trajectory ( $\theta$ ) and of head angular velocity in space ( $\alpha$ ) are displayed in the right panels. Time zero corresponds to the instant when the corner position is reached. Note nystagmus is more evident at light than in darkness. Recordings refer to the epoch when the subject crossed the sampling volume.

reciprocal of local radius) attained a maximum. In case two successive curvature peaks appeared, the midpoint between them was taken. Mean head orientations, eye movements and walking directions for the study population were then computed over time, starting backwards and forwards from the time when the subjective corner positions was reached.

Fig. 1 shows the results of the analysis from one subject. Gaze points to final position much before the corner position is attained and realigns with walking direction afterwards. All signals start to rise from baseline more than 1 s before the corner is reached in FW (both in light and dark), attain a maximum near the corner time and return to the baseline afterwards. In BW they tend to leave the baseline less than 1 s before the corner time. Eye movement amplitude tends to be greater in FW than in BW. Notice the presence of nystagmus in all diagrams, with rapid phases directed toward the direction of steering, that is to the right in FW and to the left in BW, independent of the visual condition. EOG and  $\alpha$  show a similar time course.

Fig. 2 shows average trajectories and direction time series from all subjects in all conditions. When computing EOG

means across trials and subjects, rapid eye movement phases cancel out. Thus, unlike the preceding figure, gaze orientation shows smooth changes. The anticipation relative to the corner position is nevertheless well described by mean waveforms. Global means confirm the description given for the individual subject. Note that mean  $\theta$  tends to be close to the baseline in BW locomotion, especially in the dark. All signals have lower amplitude in BW. Anticipatory movements of head and eyes develop starting from more than 1 s before the corner position is attained in FW locomotion essentially independent of whether subjects could see or not. Conversely, in BW the anticipation develops less than 1 s before the corner. Also the peaks in the time series occur before the corner time in FW and exactly at the corner time in BW. The direction of anticipatory movement coincides with the direction of steering.

Mean walking speed were the following (mean  $\pm$  SD):  $1.15 \pm 0.15$  m/s in light FW,  $1.11 \pm 0.26$  in dark FW,  $0.96 \pm 0.21$  in light BW and  $0.85 \pm 0.23$  in dark BW. Two-way within-subjects ANOVA (locomotion direction by visual condition) shows that only direction yields a sig-

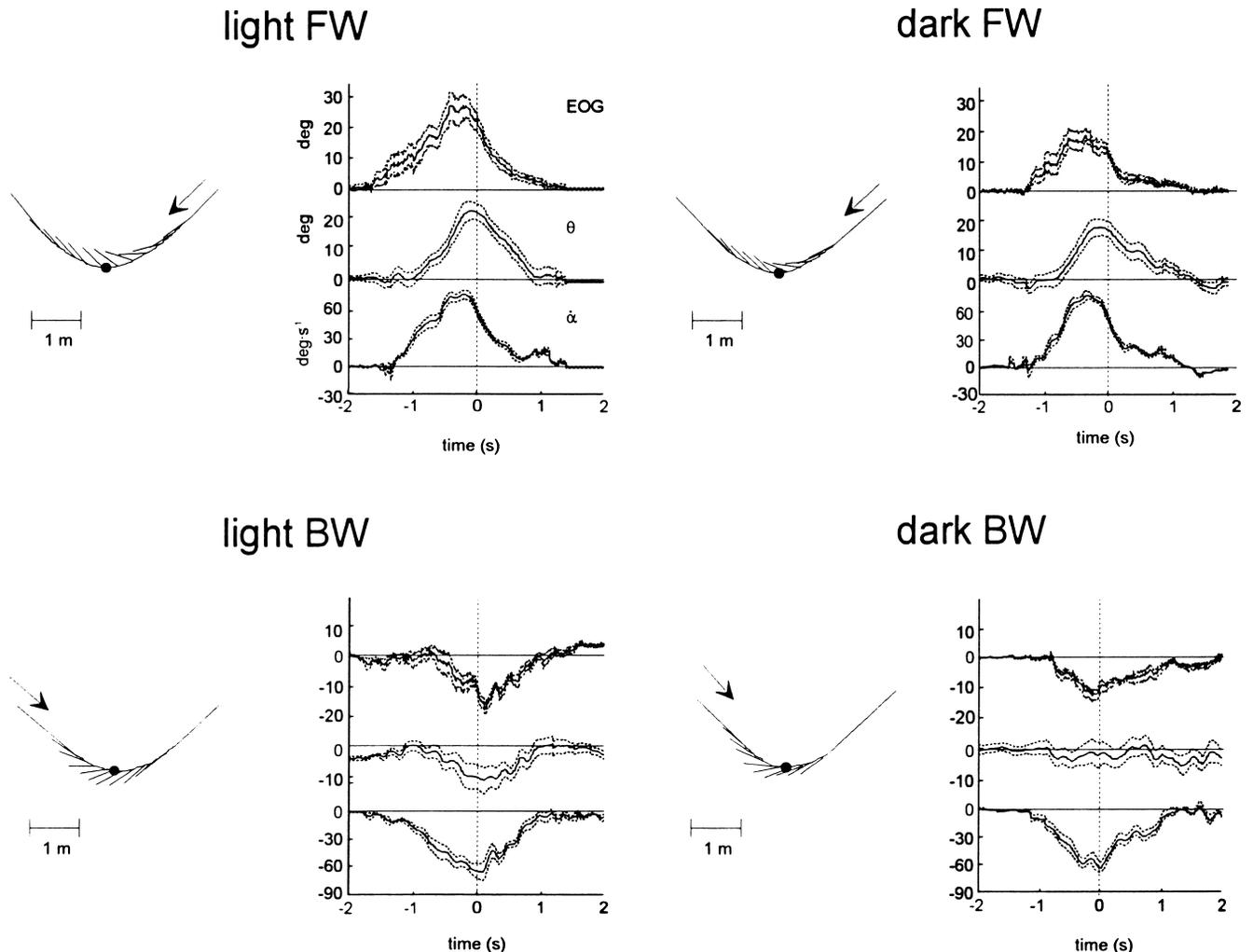


Fig. 2. Results. Global means  $\pm$  SEM are displayed using the same conventions of Fig. 1. SEM lines are displayed around the corner position (when all subjects were included in the analysis), not at the trajectory extremes.

nificant difference, ( $P < 0.01$ ) independent of the visual condition (interaction was not significant).

For  $\theta$ , the standard error is greater in BW locomotion, especially in dark. This reflects large interindividual variability in head and eye movements. Indeed, some subjects displayed little anticipation while walking BW and their gaze orientation changes peaked after the corner was reached.

This study shows that coherent head and eye movements sustain a gaze orientation synergy during physiological (FW) navigation tasks. Anticipation occurs relative to the direction one is about to take. In absence of visual stimuli, the orienting movements show similar behaviour. However they cannot be considered as inscribed in a general motor pattern for curvilinear locomotion as, after inverting the locomotor direction, they are not maintained. Actually, either they disappear or they are reversed according to the direction of steering.

Such orienting synergies probably result from complex physiological mechanisms comprising voluntary and reflex pathways. Smooth pursuit and optokinetic nystagmus were allowed at light and could sum to the vestibular and proprioceptive [2] inputs. Strikingly, only quantitative differences allow differentiating between the two visual conditions, calling for a common explanation.

Proprioceptive and vestibular cues may have been used to update an internal image of the target-to-be-reached that could evoke a virtual visual tracking. In BW locomotion, this mechanism cannot be proposed, as the target belongs to the back, non-visual, space (it is worth mentioning that, in BW, no subject pursued the starting position).

Axial orienting synergies may also explain the observed behaviour: the rapid phases of eye movements, which are directed toward the direction into which the head is turning are known to be genuine anticipatory orienting reactions elicited by head rotation in space and aimed at specific points of interest [3]. This mechanism can indeed predict the direction of gaze in both FW and BW motion, although it cannot perfectly account for the observed FW-BW asymmetries (the amplitude differences in head angular velocity between FW and BW are lower than those shown by  $\theta$  and EOG).

The results of this study confirm the observation of previous experiments [5,7] and add evidence to the hypothesis of a feed-forward navigation control system governing synergic head and eye movements aimed at anticipating future motor events. Such synergies, although complex, may belong to phylogenetically old neural mechanisms gen-

erating basic axial orienting patterns. Anticipatory orientation would allow for achieving a stable frame of reference in time to effectively program and execute action. In fact, Patla et al. [9] have shown that a new direction in locomotion needs to be programmed one step in advance in order to overcome the delays due to biomechanical inertia. Some neurophysiological bases that may explain the anticipatory triggering of orienting reactions may lie in the neural networks governing head direction in space during navigation. Blair and Sharp [1] found that the directional tuning of head direction cells in the antedorsal nuclei of rat thalamus systematically displays anticipatory shifts toward the future direction of the head in space. Recent findings account for the presence of similar networks in the primate brain [10].

This research has been performed in the frame of the European Laboratory of Action Neuroscience (LENA) and was partially supported by the Galileo project, Ministère des affaires étrangères–Conferenza dei Rettori delle Università Italiane (France-Italy).

- [1] Blair, H.T. and Sharp, P.E., Anticipatory head direction signals in anterior thalamus: evidence for a thalamocortical circuit that integrates angular head motion to compute head direction, *J. Neurosci.*, 15 (1995) 6260–6270.
- [2] Bles, W., de Jong, J.M.B.W. and de Wit, G., Somatosensory compensation for loss of labyrinthine function, *Acta Otolaryngol.* (Stockh.), 97 (1984) 213–221.
- [3] Chun, K.S. and Robinson, D.A., A model of quick phase generation in the vestibuloocular reflex, *Biol. Cybern.*, 28 (1978) 209–221.
- [4] Ferrigno, G. and Pedotti, A., ELITE: a digital dedicated hardware system for movement analysis via real-time TV signal processing, *IEEE Trans. Biomed. Eng.*, 32 (1985) 943–950.
- [5] Grasso, R., Assaiante, C., Prévost, P. and Berthoz, A., Development of anticipatory orienting strategies during locomotor tasks in children, *Neurosci. Biobehav. Rev.*, 22 (1998) 533–539.
- [6] Grasso, R., Bianchi, L. and Lacquaniti, F., Motor patterns for human gait: forward versus backward locomotion, *J. Neurophysiol.*, (1998) in press.
- [7] Grasso, R., Glasauer, S., Takei, Y. and Berthoz, A., The predictive brain: anticipatory control of head direction for the steering of locomotion, *NeuroReport*, 7 (1996) 1170–1174.
- [8] Land, M.F. and Lee, D.N., Where we look when we steer, *Nature*, 369 (1994) 742–744.
- [9] Patla, A.E., Prentice, S.D., Robinson, C. and Neufeld, J., Visual control of locomotion: strategies for changing direction and for going over obstacles, *J. Exp. Psychol. Hum. Percept. Perform.*, 17 (1991) 603–634.
- [10] Robertson, R.G., Rolls, E.T. and Georges-François, P., Spatial view cells in the primate hippocampus: effects of removal of view details, *J. Neurophysiol.*, 79 (1998) 1145–1156.