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RESEARCH ARTICLE

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"Look where you're going!": gaze behaviour associated with maintaining and changing the direction of locomotion

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Abstract In order to fully understand how vision is used to guide locomotion it is necessary to know what people look at as they move through the environment. This study provides information, hitherto lacking, regarding gaze behaviour associated with both maintaining and changing the direction of locomotion: activities that are essential for efficient navigation through our cluttered environment. Participants' spatiotemporal gaze patterns were recorded whilst they performed a task requiring that they either maintained a straight walking trajectory or changed their direction of walking by 30° or 60°, left or right, at the midpoint of a 9-m path. Participants were either visually cued to turn when they stepped on a trigger mat placed one step before the mid-point of the walkway (cued trials) or given verbal instruction about the required route prior to the start of each trial (advance knowledge trials). Our clear finding was that for the large majority of the time participants' gaze was aligned with environmental features lying in their current plane of progression both prior to and following the onset of the transition stride during which the direction change was implemented. This gaze behaviour was observed both during cued trials (78% of total fixation time prior to the transition stride onset and 89% following the transition stride onset) and advance knowledge trials (67% prior to transition stride onset, 92% following transition stride onset). When not aligned with the plane of progression, gaze was normally fixated on environmental features related to either known or potential future routes. Prior to changing the direction of walking, individuals invariably made saccadic eye movements in order to align gaze with the end-point of the required travel path. This gaze realignment was invariably accompanied by head reorientation, which was initiated, on average, at the same time as the saccade. On average, participants fixated gaze on their goal (represented by the cue light at the travel path end-point) until after head realignment with the new path was achieved. Additionally, the head was consistently aligned with participants' current walking direction prior to and following the transition stride even on the minority of occasions when they were looking elsewhere. These findings challenge the ecological validity of existing theories of how visual information is used to determine heading direction and are consistent with the proposal that aligning the head with the desired travel direction through coordinated eye and head movements provides the CNS with an allocentric frame of reference that is used to control the movement of the body in space.

Keywords Heading · Steering-eye movements · Vision

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Introduction

Vision is the only human sensory modality capable of providing information about distant environmental features. This unique characteristic makes it possible for visual information to be used in a feedforward manner to modulate gait patterns, thereby allowing walking individuals to avoid obstacles in their travel paths or to reach specific goals in the environment. Although it is universally accepted that vision plays important roles in guiding locomotion, there is still a great deal of controversy regarding the precise nature of visual information that is used. In order to fully understand how vision is used to guide locomotion it is necessary to know: what visual features people look at, when people look at them, where people are in relation to these features when they look at them and how people bring the retinal field to the target of interest.

Most studies of visually guided locomotion have described whole body and/or head movement and used this information to infer where the eyes were targeted (Pozzo et al. 1995; Grasso et al. 1998; Patla et al. 1999). Several studies have monitored the eyes during locomotion (Hollands and Marple-Horvat et al. 1995, 2001; Hollands and Marple-Horvat 1996; Crowdy et al. 2000), but these were limited to measurements of the horizontal components of eye movements during a precision stepping stone task that generated predictable gaze patterns.

Grasso et al. (1998) monitored both the head and horizontal eye movements of individuals walking around corners and showed that during the turn individuals made anticipatory eye and head movements to align with their future walking trajectory even with their eyes closed. Imai et al. (2001) recently extended these findings by performing a comprehensive three-dimensional analysis of body, head and eye movement behaviour of participants walking around corners. The results clearly showed that combined yaw, pitch and roll movements of the body, head and eyes maintain gaze in the direction of forward motion during straight walking and direct gaze in advance of the heading trajectory during turning. However, only average gaze position calculated with respect to individuals' walking trajectories was described and therefore no information was provided about which environmental features participants were looking at prior to, during and following the turn.

The only published study to provide information on gaze patterns is that of Patla and Vickers (1997), who used a purpose-built gaze tracking system to study the gaze behaviour of participants required to walk towards and step over an obstacle in their travel path. They discovered that subjects fixated the obstacle during the approach phase and *not* during the step over it. When not fixating the obstacle participants spent most of the time 'travel fixating': gaze behaviour characterised by eye stabilisation with respect to the direction of locomotion. This description of gaze behaviour provided by this study has contributed to our understanding of the visuomotor control strategies used in obstacle clearance. However, there are currently no published studies documenting gaze behaviour associated with other everyday locomotor activities.

Arguably, one of the most fundamental roles vision plays during locomotion is in the control of steering, i.e. controlling the direction of walking or running to reach (or avoid) certain environmental features. Steering paradigms have been widely used by researchers of visual perception to test theories of how humans extract heading information from the visual field. Investigations of the control of heading were revolutionised by the development of optic flow theories in the 1950s which proposed that the patterns of light reaching the eye generated by self-motion can be used to estimate heading. Gibson (1950, 1966) argued that the centre of expansion of the optic flow field reaching the eye specifies a walking observer's heading and therefore to reach a target one need simply keep the target as the focus of expansion: the region of the optic flow field that is not moving. However, in practice, optic flow field projects onto a *retinal* flow field, which has two components, a linear flow field generated by body movement (whose centre of expansion specifies heading), and a rotary field generated by head and eye movements. For example, when an individual walks straight while fixating gaze on an environmental feature lying to one side, the retinal flow generated will contain linear or translational flow produced by their forward progression and rotary flow generated by compensatory eye rotations that serve to stabilize gaze on the feature of interest. A central theme in studies of heading judgements has been whether the retinal flow field can be decomposed to recover the translation component of locomotion when flow also contains the effects of eye rotation (see Lappe et al. 1999 for review). Psychophysical studies have demonstrated that to solve the decomposition problem due to eye rotations the visual system is able to combine retinal flow analysis with many other sensory signals including efference copies of motor commands, proprioceptive signals and monocular and binocular depth cues (Lappe et al. 1999). In these studies the investigators *simulated* motion using artificial screen displays or artificially manipulated visual information and observed the effects on participants' abilities to judge heading direction. In many of these studies participants were seated and/or stationary. Although these experimental approaches have provided interesting information concerning how the CNS is able to process visual information to derive heading and solve for eye rotations, they do not tell us how vision is normally used to guide locomotion. Without knowing what walking individuals look at when moving through a real environment, it is not possible to determine how sensory information is normally used to determine heading direction.

In addition to their usefulness in investigations of visual perception, steering paradigms have provided valuable information concerning the biomechanics of changing walking direction. Specifically, they have provided evidence that neural control of head and eye movements, guided by vision, play a key role in coordination of the trunk and legs during steering. Hollands et al. (2001) studied the temporal sequence of body segment reorientation and the effect of immobilizing the head (by fixing it to the trunk) on this sequencing during a task whereby participants were visually cued to change their walking direction. The results confirmed previous findings (Grasso et al. 1996, 1998; Patla et al. 1999; Imai et al. 2001) that the head starts to turn in the new travel direction before the rest of the body. Immobilizing the head resulted, on average, in earlier onset of trunk yaw reorientation with respect to delivery of the cue to turn, suggesting that participants compensated for the loss of independent head mobility by changing the timing of their trunk reorientation, thereby realigning the head with the new travel direction in a faster time. These findings suggest that aligning the head with the new travel direction

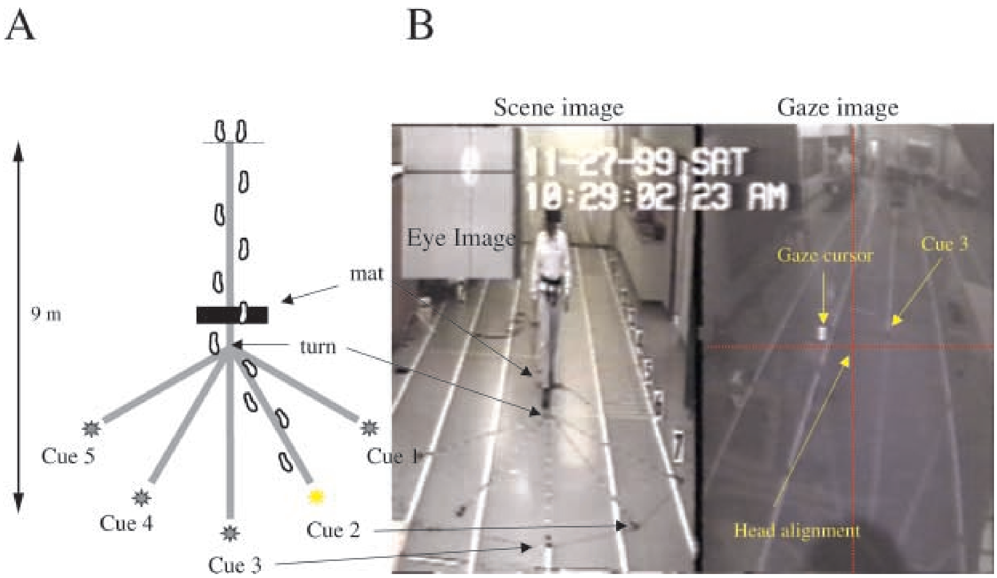

Fig. 1 **A** Schematic diagram of the steering paradigm. During the 'cued condition' trials, the required walking direction was indicated by one of five cue lights (placed at floor level) which lit up when the participant stepped on the trigger mat. During the 'advance knowledge' trials the participant was given verbal instruction to walk to a specified cue light prior to the start of the walk. The footprints represent a typical foot placement profile for a 30° left turn trial (*Cue 2*). **B** A typical video frame comprising three images: the eye image displayed at the top left of each video frame denoting the corneal reflect and centre of the pupil, the 'gaze image' displayed on the right half of the video frame showing the visual field of the participant (with the participant's gaze indicated by a white square cursor and head alignment indicated by the intersection of the red dotted lines) and the 'scene image' displayed on the left-hand side of each video frame showing a frontal view of the participant performing the task. Relevant features of the walking environment as shown in the schematic representation of the walkway **(A)** can be identified in the scene image (*black arrows*)

prior to repositioning the rest of the body is an important component of the steering strategy and not simply a consequence of whole body reorientation. However, gaze data were not collected in this experiment. Therefore, it was not possible to determine whether the observed anticipatory head movements were generated independently or as part of the gaze reorientation process.

The aim of the current study was to describe gaze behaviour of individuals performing locomotor tasks requiring both precise regulation of heading in order to follow specific routes through the environment and changing the direction of locomotion in response to visual cues. This experimental approach will not only advance our general understanding of how vision is used to guide locomotion but also provide answers to two specific questions fundamental to our understanding of steering control: first, where and when do individuals normally direct gaze when maintaining heading direction (information that will either validate or disprove current theories regarding how vision is normally used to determine heading direction during walking) and, second, are the anticipatory head rotations previously observed during direction change (Patla et al. 1999; Hollands et al. 2001) initiated independently or as part of the gaze reorientation process.

Materials and methods

Participants

Seven healthy young adults (three male, four female, mean age = 24.8±4.0, height = 1.73±6.0 m) participated in this study and received an honorarium for their involvement. Prior to testing, all participants took part in a visual acuity test using a Snellen sight chart and all were found to have 20/40 vision or better.

Data collection

Gaze behaviour data were collected using the Vision-In-Action system (VIA) (Vickers 1996), which included an Applied Sciences Laboratories (ASL) 501 eye tracker adapted for studying the coupling between vision and action. The eye tracker is a monocular corneal reflection system that measures eye line of gaze with respect to the helmet. The helmet has a 30-m cord attached to the waist, interfaced to the main computer, thus permitting the wearer near-normal mobility. Miniaturized optics (eye and scene camera), an illuminator, solid state sensor, relay lens and visor are mounted on the helmet (total weight 700 g). The participant's stepping movements were recorded simultaneously by a video camera (Sony, Model TRV82) placed in the frontal plane and interfaced to the ASL eye tracker using two digital video mixers (Videonics, Model MX-1). The 'eye image' displayed at the top left of each video frame was recorded by the eye camera on the helmet and showed the *x/y* coordinates denoting the corneal reflect and centre of the pupil. The 'gaze image' displayed on the right half of the video frame showed the visual field of the participant (normally the walkway in front) as recorded by a scene camera mounted on the helmet, with the participant's gaze indicated by a white square cursor. Spatial accuracy of the gaze was ±2.0° visual angle (one cursor width) and precision 0.5°. The 'scene image' displayed on the left-hand side of each video frame was recorded by the external camera and showed a frontal view of the participant performing the task. In this way the participant's ocular, gaze and stepping behaviours were integrated in each frame of data, at a temporal resolution of 30 Hz or 33.33 ms/frame. Figure 1B shows a typical video frame showing the three images: scene, gaze and eye. A microphone worn by the participants recorded their verbal comments on the VIA video. A calibration procedure required each participant to fixate on each of nine points of a matrix placed in the frontal plane. This was followed by a fine calibration performed before and after each trial, relative to a set of reference points in the travel path. During collection the VIA data were continually monitored to allow any problems to be detected and rectified.

Protocol

Participants walked at their natural self-selected pace along a 9-m straight travel path. For 50% of trials, which we will refer to as the cued condition, at the mid-point of the travel path subjects were visually cued to turn via lights placed on the floor at the end of each pathway (Fig. 1A). During these trials participants were required to either continue walking straight or to alter direction by either 30° or 60° to the left (counterclockwise) or to the right (clockwise). Light cues were activated when participants stepped on a pressure-sensitive mat placed one step length before the mid-point of the straight travel path such that the participant had one stride duration (two steps) to plan and implement a direction change. Participants were instructed to start walking with either their left or right leg depending on the required turn direction so that they were never required to cross one leg in front of the other in order to turn successfully. Although the required turn direction was always towards the same side as the leg with which participants were instructed to start walking, participants did not behave as if they were aware of this. When debriefed at the end of the experiment all subjects reported that they did not notice this pattern.

In addition to the cued condition participants performed trials whereby they were verbally instructed at the start to walk towards a specified cue light location (advance knowledge condition). Each subject performed 20 trials in total, two towards each of the five cue light locations for both experimental conditions. Presentation of trials was fully randomized. The protocol was approved by the University of Calgary Ethics Committee.

Data analysis

Video data were coded in an editing suite containing video-playing equipment capable of frame by frame shuttle control. Gaze behaviour was categorised as: (a) fixation on a location or object within the video scene, (b) travel fixation or (c) a shift in gaze from one location to another. Fixation was defined as the stabilisation of gaze on a location in the environment for three frames (99.9 ms) or longer (see Vickers 1996). Travel fixation was defined as a shift in gaze caused by whole body movement (three frames minimum duration). Gaze was stabilized at a constant distance in front of the participants' body and moved in the same direction and at the same speed as locomotion. Change in gaze location was always achieved via saccadic eye movements. A saccade was defined as a rapid eye movement (between two and four frames in duration) causing a shift in gaze between two locations and was easily identified from the image of the eye in the top left corner of the frame (see Fig. 1B). The gaze scene on the right-hand side of each frame showing the participant's viewpoint (on which the gaze cursor was superimposed) was generated by a camera mounted on his/her helmet. The image lying along the midlines of this scene corresponded to the direction in which the participant's head was pointing. Therefore, when the gaze cursor was positioned at the point where the midlines of this scene intersect, the right eye was in a central position in orbit and the gaze was pointing in the same direction as the head. Since the required travel path was indicated by marker tape at floor level, head alignment with (and rotation away from) the required travel direction was easily identified. Times of left and right toe-off, defined as the points in time when the left and right foot left the floor (indicating the onset of the swing phase), were also identifiable from the scene image on the left-hand side of the frame (Fig. 1B).

For each trial all gaze behaviours (including fixation locations) were identified and documented at every step. The following fixation locations were identified (Fig. 1A): cue lights (numbered 1–5), trigger mat, turn point (where required path deviates from a straight path), branch of new path (floor directly between turn point and cue light), and heading (point beyond cue light along plane of progression). The percentage of total fixation time participants fixated gaze on each location was calculated and mean values determined. Data were separated into two groups according to when, during the trial, it was collected: prior to and following transition stride onset (defined as the instant of cue delivery in the cued condition and as the instant of contralateral toe-off (CTO) (Fig. 1) in the advance knowledge condition. Note that in the cued condition, the onset of the transition stride was defined as the moment of cue delivery, which was easily observable from the video data. We know that cue delivery occurred when the participant's heel contacted the trigger mat. However, since it was not possible to accurately determine heel contact from the video data, in the advance knowledge condition in which there was no cue delivery, onset of transition stride was defined as CTO following ipsilateral heel contact. Therefore there was a systematic error of one double support phase (the time interval between ipsilateral limb heel contact and contralateral limb toe-off) in our determination of transition stride onset in the advance knowledge condition. The average double support phase duration is approximately 2 frames or 66.6 ms. Since the average duration of a walk was in the order of 5 s, then this error in estimation represents only around 1% of the total fixation time. Latencies with respect to cue delivery/CTO of onset of head and gaze realignment with the new path were calculated for each trial in which subjects were required to turn.

Results

Example of gaze behaviour: cued condition

Figure 2A shows an example of the temporal gaze pattern obtained from a single cued condition trial. The *y*-axis corresponds to the various environmental features that the participant fixated frame by frame and the *x*-axis corresponds to the frame number. The horizontal lines represent contiguous frames in which gaze was fixated on the same feature. For example the yellow line joining frames 43 and 53 demonstrates that cue light three was fixated for ten frames (333 ms) between these times. The lines cannot overlap since it is not possible to foveate more than one feature at a time. Frames without data (e.g. 10–13) correspond to times whereby gaze was either in transit between two features or obscured due to eye blinks. The vertical dashed line indicates the frame in which the cue to change direction was delivered.

Figure 2B shows the corresponding example of gaze data obtained from a single advance knowledge trial. In this case the vertical dashed line indicates the time of CTO.

Gaze behaviour during cued condition

Prior to cue delivery

Table 1 lists the mean values of the total percentage of time prior to onset of the transition stride (cue delivery) that participants fixated various environmental features. During this part of the trial participants were required to maintain a straight walking trajectory. Mean gaze fixation duration is expressed as a percentage of total fixa-

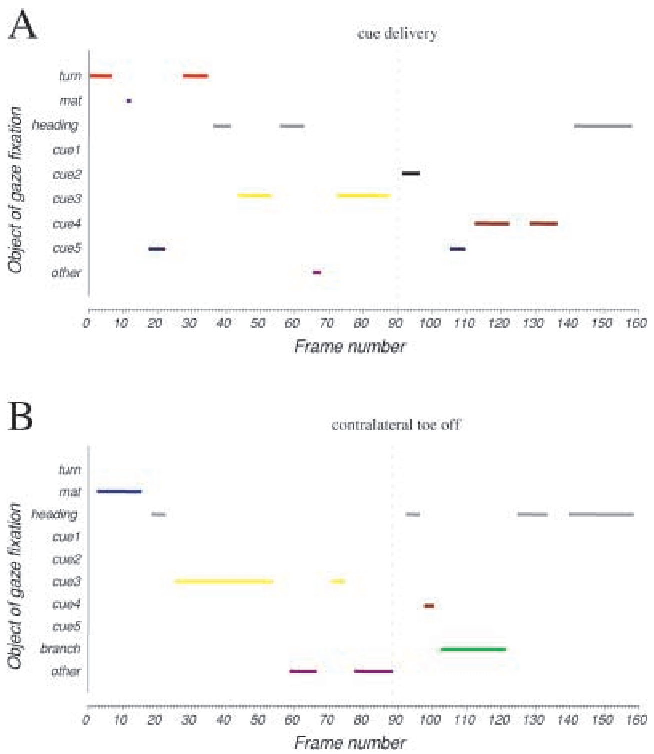

Fig. 2 **A** An example of the temporal gaze pattern obtained from a single cued condition trial. The *y*-axis corresponds to the various environmental features that the participant visually fixated frame by fame and the *x*-axis corresponds to the frame number. *The coloured horizontal lines* represent contiguous frames in which gaze was fixated on the same feature. *The vertical dotted line* indicates the frame during which the cue was delivered (cue light 4 lit up), which coincided with the participant stepping on the trigger mat. **B** Same information as presented in **A** for a single advance knowledge trial in which the participant was instructed to walk to cue 4. *The vertical dotted line* indicates the onset of the transition stride characterised as toe-off of the limb contralateral to the turn direction (CTO)

tion time. The data were separated into two categories according to whether or not the visually fixated environmental feature lay in the participant's current plane of progression.

Cue3 was fixated for the longest time (47.4% total); trigger mat fixation, fixation of points in the distance (beyond cue3) and travel fixation each accounted for approximately 10% of total fixation time. The turn point was fixated for around 2.5% of total time. Each of these environmental features lies along the straight path. Therefore, the majority of the time (78.8%) was spent fixating aspects of the environment lying along their cur-

Table 1 Mean durations that participants fixated gaze on each environmental feature both prior to and following the onset of the transition stride (cue delivery) and for both the cued and the advanced knowledge conditions. Mean gaze fixation duration is expressed as a percentage of total fixation time. *The values on the left-hand side of the table* correspond to the total duration of visual fixation of features lying in the participants' current heading direction. *The values on the right side of the table* correspond to the total duration of visual fixation of features lying in an eccentric location with respect to current heading direction

Current heading				Other			
Gaze direction	% total gaze fixation	SD	*N*	Gaze direction	% total gaze fixation	SD	*N*
Cued condition: prior to cue delivery							
Cue 3	47.4	26.1	80	Other cue	16.3	17.9	80
Travel fixation	10.5	24.9	80	Other	4.9	8.6	80
Heading	9.4	16.6	80				
Trigger mat	9.1	12.5	80				
Turn	2.5	5.3	80				
Total	78.8	20.2	80	Total	21.2	20.2	80
Cued condition: after cue delivery							
Right cue	53.0	27.0	80	Other cue	8.8	10.3	80
Heading	28.4	25.6	80	Other	1.7	4.3	80
Branch	7.1	16.9	80				
Travel fixation	1.1	5.9	80				
Total	89.5	10.7	80	Total	10.5	10.7	80
Advance knowledge condition: prior to transition stride							
Cue 3	18.7	24.6	69	Right cue	22.0	31.6	69
Heading	17.5	22.9	69	Branch	5.0	8.4	69
Turn point	12.2	16.1	69	Other	4.7	11.1	69
Travel fixation	9.4	21.6	69	Other cue	1.2	3.9	69
Trigger mat	9.2	14.8	69				
Total	67.0	30.5	69	Total	33.0	30.5	69
Advance knowledge condition: after transition stride							
Right cue	44.6	32.1	69	Other	4.3	11.7	69
Heading	32.9	28.0	69	Cue 3	2.9	8.5	69
Branch	13.4	23.2	69	Turn point	0.5	2.9	69
Travel fixation	1.0	8.0	69	Other cue	0.3	1.9	69
Total	91.9	14.1	69	Total	8.1	14.1	69

rent plane of progression (straight heading direction); the rest was spent visually inspecting possible future routes, i.e. other cue lights (16.3%) or looking at what appeared to be random points in the room (4.9%).

The result of a paired *t*-test showed that the mean duration of gaze fixation on environmental features lying in participants' current plane of progression was significantly longer than duration of gaze fixation on other environmental features (*T*=12.77, *P*<0.001).

Following cue delivery

Table 1 also lists the mean values of the total percentage of time *after* onset of the transition stride (cue delivery) that participants fixated various environmental features. During this part of the trial subjects were required to identify the required travel direction and implement a turn in that direction. The appropriate cue light was fixated most of the time (53% total), fixation of points in the distance (beyond the appropriate cue light) accounted for 28.4% of total fixation time, and 7.1% of time was spent visually inspecting the part of the floor lying directly between the turn point and the cue light. Only 1.1% of time was spent travel fixating.

Therefore, again, the majority of the time (89.5%) was spent fixating aspects of the environment lying in the new heading direction, the rest being spent either looking for the appropriate cue light (8.8%) or looking at what appeared to be random points in the room (1.7%). The result of a paired *t*-test showed that the mean duration of gaze fixation on environmental features lying in participants' current plane of progression was significantly longer than duration of gaze fixation on other environmental features (*T*=32.9, *P*<0.001)

Gaze behaviour during advance knowledge condition

Prior to start of transition stride

During this part of the trial subjects were required to maintain a straight walking trajectory. The large majority of the time (67%) was spent fixating aspects of the environment lying along their current plane of progression (turn point, mat, cue3, heading and travel fixation), the rest (27%) being spent visually inspecting their future route (right cue and branch), looking at other cue lights (1.2%) or looking at what appeared to be random points in the room (4.7%).

The result of a paired *t*-test showed that the mean duration of gaze fixation on environmental features lying in participants' current plane of progression was significantly longer than duration of gaze fixation on other environmental features (*T*=4.64, *P*<0.0001).

Following transition stride

The bottom section of Table 1 lists the mean values of the total percentage of time *after* CTO that participants fixated various environmental features. During this part of the trial subjects were required to implement a turn in the required direction. The vast majority of the time (91.9%) was spent fixating aspects of the environment lying in their new heading direction (cue light, branch or ahead in distance), the rest being spent either fixating cue3 prior to turning (2.9%) or looking at what appeared to be random points in the room (4.3%).

The result of a paired *t*-test showed that the mean duration of gaze fixation on environmental features lying in participants' current plane of progression was significantly longer than duration of gaze fixation on other environmental features (*T*=24.7, *P*<0.0001).

Variation in gaze behaviour between individual participants

To assess the extent of differences in gaze behaviour exhibited by individual participants, mean values of the total time spent fixating environmental features lying in the current heading direction were calculated for each subject. These are presented in Table 2. The results demonstrate that each participant showed the same general trend in gaze behaviour, i.e. for the large majority of the

Table 2 Mean values for each participant of the mean gaze fixation duration (expressed as a percentage of total fixation time) of features lying in the participants' current heading direction

Subject	Cued condition: prior to cue delivery			Cued condition: after cue delivery			Advance knowledge condition: prior to CTO			Advanced knowledge condition: after CTO		
	Mean % total gaze fixation	SD	*N*	Mean % total gaze fixation	SD	*N*	Mean % total gaze fixation	SD	*N*	Mean % total gaze fixation	SD	*N*
1	54.4	24.2	12	86.9	10.2	12	46.1	30.9	10	93.3	10.5	10
2	72.8	20.7	12	93.1	7.7	12	66.5	40.7	10	80.6	21.1	10
3	87.8	13.5	10	97.3	4.8	10	50.3	38.0	10	91.7	16.0	10
4	81.3	13.4	12	85.9	8.3	12	63.8	23.6	10	95.8	7.2	10
5	86.5	14.4	11	91.8	10.7	11	78.6	9.8	10	100.0	0.0	10
6	96.9	8.8	11	86.1	17.7	11	80.4	19.2	9	96.6	6.0	9
7	75.9	12.7	12	86.8	8.7	12	84.8	22.3	10	85.6	17.4	10

time he/she aligned gaze with features lying in his/her current heading direction. The only exception to this trend was subject 1, who, in the 'advanced knowledge: prior to CTO condition', spent slightly less than half of the total fixation time looking at features lying in the current heading direction.

Head orientation

In both experimental conditions head yaw deviations from the straight path prior to the transition stride and from the new path once head reorientation was achieved were minimal. In every trial the participant's head was consistently aligned with their current walking direction even when gaze was fixated elsewhere.

Gaze and head reorientation with new travel path: cued condition

Latency of eye and head reorientation onset with respect to cue delivery

All participants invariably made a saccadic eye movement so as to fixate the appropriate cue light after it lit up. Gaze refixation was always accompanied by head reorientation. The mean latency of reorientation onset with respect to cue delivery was 326 ms for the eye (SD=237 ms, *N*=52) and 349 ms for the head (SD=210 ms, *N*=52). In other words, on average, both eye and head reorientation onset followed cue delivery by around 350 ms. The results of ANOVA demonstrate that there was no significant main effect of body part (eye or head) on the mean latency of reorientation onset ($F_{(1,6)}$=1.26, P>0.05).

There was, however, a significant main effect of required turn magnitude (30° or 60°) on the mean latency of reorientation onset ($F_{(1,6)}$=11.75, P<0.05). The mean latency of reorientation onset with respect to cue delivery was 263 ms (SD=170 ms, *N*=50) for 30° paths (cue lights 2 and 4) and 407 ms (SD=250 ms, *N*=54) for 60° paths (cue lights 1 and 5).

There was no significant interaction between body part and turn magnitude on the mean latency of reorientation onset ($F_{(1,6)}$=1.65, P>0.05).

Completion of eye and head reorientation

Mean interval between termination of head rotation and end of gaze fixation on a cue light was 170 ms (SD=630 ms, *N*=52). In other words, on average subjects fixated their gaze on a cue light until 170 ms *after* head realignment with the new heading direction was completed.

Gaze and head reorientation with new travel path: advance knowledge of route

Latency of eye and head reorientation onset with respect to CTO

When participants were given knowledge of their required route prior to starting walking, head and gaze realignment with the appropriate path again invariably preceded a change in walking direction. The mean latency of reorientation onset with respect to CTO was –40 ms for the eye (SD=371 ms, *N*=48) and –50 ms for the head (SD=317 ms, *N*=48). In other words, on average, reorientation onset of both the eye and head preceded CTO by around 50 ms. The results of ANOVA analysis demonstrated no significant main effect of body part (eye or head) on the mean latency of reorientation onset ($F_{(1,6)}$=0.39, P>0.05).

There was, however, a significant main effect of required turn magnitude (30° or 60°) on the mean latency of reorientation onset ($F_{(1,6)}$=9.10, P<0.05). The mean latency of reorientation onset with respect to CTO was –145 ms (SD=340 ms, *N*=48) for 30° paths (on average, orientation onset preceded CTO) and 55 ms (SD=320 ms, *N*=48) for 60° paths (on average, orientation onset followed CTO).

There was also a significant interaction effect between body part and turn magnitude on the mean latency of reorientation onset ($F_{(1,6)}$=33.53, P<0.05). Figure 3 shows the mean latency of reorientation onset for each turn magnitude and body part. Significant differences as revealed by post hoc analysis (Bonferroni) are indicated by asterisks.

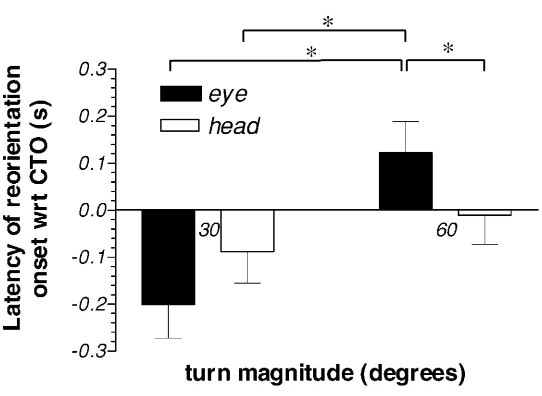

Fig. 3 Bar chart to show the mean latency of reorientation onset for each turn magnitude and body part in the advance knowledge condition. *Filled bars* show mean eye latencies and *unfilled bars* mean head latencies. Contralateral toe-off (*CTO*) is at time zero. *Bars with positive values* correspond to movement onsets that occur after CTO and *bars with negative values* to movement onsets that occur prior to CTO. Significant differences as revealed by post hoc analysis are indicated by *asterisks*

Completion of eye and head reorientation

As with the cued condition, the mean interval between termination of head rotation and end of gaze fixation with the appropriate cue light was 170 ms (SD=680 ms, N=49).

Discussion

Determination of heading from retinal flow fields

This is the first study to continuously measure gaze behaviour associated with maintaining heading and changing the direction of walking. Our clear finding is that participants' gaze was consistently aligned with environmental features lying in their current plane of progression, prior to, and following, a change in walking direction. This gaze behaviour was observed both during trials in which participants were given advance knowledge of their route prior to the start of the walk and during trials in which participants were cued to change walking direction at short notice. These findings are consistent with the results of analyses of eye, head and body interactions during straight walking and turning (Grasso et al. 1998; Imai et al. 2001) and have important implications for theories regarding how vision is used to control heading.

A central theme in studies of heading judgements has been whether the retinal flow field can be decomposed to recover the translation component of locomotion when flow also contains the effects of eye rotations (Longuet-Higgins and Prazdny 1980, Regen and Beverley 1982; Warren and Hannon 1988, Lappe et al. 1999). The results of the present study, which is the first to provide detailed information about where we look during steering of locomotion, suggest that we do not normally have to perform the complex decomposition of flow fields. When individuals' eyes and head are aligned with environmental features lying in their direction of travel, as demonstrated by participants in the present study, yaw rotary components of optic flow are not generated since there are no horizontal eye rotations. There are rotary components in the retinal flow fields generated by compensatory *vertical* eye rotations. For example, Fig. 2A shows that at frame 30 the participant fixated the turn point (see Fig. 1) for six frames (approximately 180 ms). During this time period the participant was continuously moving forward with respect to this environmental feature. Therefore, for the participant to maintain gaze on the turn point during this forward translation it would have been necessary to vertically rotate the eyes (change pitch angle) to compensate for the ongoing change in head position with respect to the turn point. Although these compensatory eye rotations generate rotary flow, resulting in the focus of expansion being shifted *vertically* with respect to the direction of heading, the focus of expansion and the heading direction remain in the same *horizontal* plane. Therefore, walking towards the focus of expansion of retinal flow will result in participants reaching their target destination. Since there is no yaw rotational component to remove from retinal flow under these circumstances, then decomposition of linear and rotary components of optic flow fields is not necessary. Therefore, our findings challenge the ecological validity of psychophysical studies of optic flow decomposition problems and allow for the possibility that the focus of expansion of optic flow patterns is used by walking individuals to control heading as first proposed by Gibson (1966). It should be stressed, however, that our findings are equally compatible with recent theories that question whether retinal flow is used in the visual guidance of locomotion (Rushton et al. 1998). These are described in the next section.

Egocentric control of walking

Recent evidence that challenges the need for optic flow in controlling the direction of locomotion has been provided by Rushton et al. (1998), who used displacing prisms to alter optic flow patterns by 16° as participants walked across a grass lawn towards a target. The investigators interpreted the finding that subjects took a distinctive curved path to reach the target under these conditions as evidence that participants were determining heading direction based on perception of visual direction of the target in relation to the body rather than flow information. The authors proposed that participants' misperception of the location of the target relative to their body resulted in constant misalignment of their locomotor axis with the true direction of the target to produce a constant heading error. This proposed strategy of navigation is supported by our current findings. We have clearly demonstrated that prior to changing the direction of locomotion to reach a target, participants generate coordinated eye and head movements so as to fixate gaze on the target. It is reasonable to assume that the resulting difference between gaze direction and body midline orientation drives body reorientation with the new travel path.

Warren et al. (2001), in a recent study in which various virtual reality environments were used to manipulate participants' vision as they walked a 9-m travel path, clearly demonstrated that walking individuals are able to use both optic flow and egocentric direction control to guide goal-directed locomotion and that depending on the structure of the environment the relative weighting given to each strategy seems to change. Adopting a strategy whereby gaze is consistently directed along the locomotor axis, as demonstrated by walking individuals in our current study, would facilitate the extraction of both types of information from the visual scene. Therefore, our gaze data collected under normal conditions within a relatively richly structured environment are consistent with the suggestion of Warren et al. that both egocentric control and optic flow information are used in the normal guidance of locomotion.

Head and eyes lead the way when changing the direction of locomotion

Recent studies have demonstrated individuals walking around corners (90°) systematically direct their head and eyes toward the future direction of the curved trajectory (Grasso et al. 1998; Imai et al. 2001). Our results clearly show that prior to changing the direction of walking (by either 30 or 60°) individuals invariably made saccadic eye movements in order to align gaze with the end-point of the required travel path. This gaze realignment was invariably accompanied by head reorientation. On average, head reorientation was initiated at the same time as the saccade. The onset latency of head reorientation with respect to cue delivery measured in the current experiment was similar to the value obtained from kinematic analysis using the same experimental protocol (Hollands et al. 2001). The close timing relationship observed between eye and head reorientation onset is consistent with the proposal that anticipatory head movements are generated in coordination with eye movements as part of the gaze reorientation process. This coordinated eye and head behaviour was observed when the participants were given knowledge of their required route prior to the start of the walk in addition to trials whereby a visual cue indicating the required turn direction was delivered one step in advance. On average, participants spent less than a third of the time prior to the transition stride looking at aspects of their future travel path. Therefore, it seems that visual information about the new travel direction is most desirable immediately before it is used to implement body translation and rotation at the start of the transition stride.

The relationship between head alignment and heading

Participants usually fixated gaze on their goal (represented by the cue light at the travel path end-point) until after head realignment with the new path was achieved. Additionally, the head was consistently aligned with participants' current walking direction prior to and following the transition stride even when they were looking elsewhere. These clear findings are consistent with the proposal that aligning the head with desired travel direction through coordinated eye and head movements provides the CNS with an allocentric frame of reference that can be used to control the rest of the body. Similar hypotheses have been proposed by Pozzo et al. (1990, 1992, 1995), who described periods of head stabilisation in space during diverse locomotor tasks ranging from normal forward walking to backward somersaulting. Imai et al. (2001) recently confirmed the findings of Grasso et al. (1998) that participants walking around a corner anticipated the turn by directing gaze (via coordinated head and eye movements) about the yaw axis and demonstrated that changes in the sum of the linear accelerations acting on the head (gravitoinertial accelerations or GIA) are anticipated by rotating the head in the pitch and roll axes relative to heading. These findings suggest that anticipatory head and eye movements play important roles in the steering of locomotion. Hollands et al. (2001) recently reported that immobilizing the head during steering resulted in compensatory changes to the timing of trunk reorientation. This finding provides evidence that proactive head realignment is itself important for steering control in addition to its role in gaze realignment and stabilisation. The authors proposed a hierarchical schema whereby a visual image of a locomotor goal is first visually fixated via saccadic eye movements, providing a gaze-centred frame of reference that can be used to align the head with the goal. Head realignment, in turn, provides the CNS with a head-centred frame of reference that is used to control body reorientation. The results of the current study are consistent with this proposal.

The aforementioned studies suggest that the neural control of head and eye movements, guided by vision, plays a key role in coordination of the trunk and legs. It is not surprising that head position in space is implicated as a reference for the coordination of other body parts. The head contains both vestibular and visual apparatus, which are arguably the richest sources of information describing our position with respect to our environment. In addition the neck contains extensive numbers of muscle spindles providing accurate proprioceptive information describing the position of the head with respect to the trunk (Cooper and Daniel 1963). Indeed, neurophysiological studies have identified 'head direction cells' that fire selectively when the head is pointed in a specific direction in space in the thalamus and postsubiculum of rats (McNaughton et al. 1996) and in the primate presubiculum (Robertson et al. 1999). Therefore reorienting the head in the new travel can provide the CNS with both an allocentric and an egocentric reference frame that can be used to reorientate the rest of the body.

Conclusions

This study investigated gaze behaviour associated with maintaining and changing heading direction: activities that are essential for efficient navigation through our cluttered environment. The observed gaze and head movement behaviour challenges the ecological validity of popular theories regarding how visual information is used to determine heading direction and is consistent with the proposal that aligning the head with the desired travel direction through coordinated eye and head movements provides the CNS with an allocentric frame of reference that is used to control the movement of the body in space.

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