

Multisensory Interactions Concerning Human Self-motion

Thesis for the qualification of PhD

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Abstract of Thesis

Humans move in their environment and have a number of different sources of information about their self-motion, e.g. visual, vestibular, proprioceptive and somatosensory signals. These signal sources must be combined to overcome their individual limitations.

During locomotion, visual signals corresponding to object motion are distorted by motion components directly related to the speed and direction of movement by the observer. Thus, in order to allow a veridical interpretation of the visual signal by the observer, these self-motion components must be discounted, while at the same time retaining important information on their speed and progression. In experiments, the effects of proprioceptive, somatosensory and efference copy signals of self-motion are isolated by comparing the speed of a constant optic-flow stimulus that is perceived while either standing or performing a motor activity. It is found, firstly, that the more locomotion-related a motor activity may be, the greater it reduces the perceived speed. And secondly, that the more locomotion-related a visual stimulus is, the greater its perceived speed is reduced while walking. It is therefore suggested that a tuning exists between locomotor activity and the types of visual signal (i.e. optic flow) that it normally introduces.

As the eyes are mobile relative to the trunk, visual information must be reoriented to take into account gaze direction if it is to be applied usefully to control posture. The orientation of the postural response to visual motion in various directions relative to the subject is investigated using two paradigms. In the first, using passive motion of the subject in a dark room, it is difficult for subjects to cognitively reconstruct the direction of gaze, and hence, the visual motion. The data show that the postural response may take account of the gaze direction independently of cognitively mediated knowledge of the geometry of the experimental conditions. In the second, comparisons are made between the accuracy of this reorientation during the visually induced perception of self-motion (vection) and object-motion perception and it is found that the accuracy of the reorientation is improved during conscious perception of self-motion (vection).

The above experiments suggest a network of afferent (and re-afferent) self-motion signals that are combined dynamically to represent the movement of the body and its

parts. This single representation is used both to control self-motion and to compensate for its effects on other sensory processes.

Table of Contents

Thesis Abstract	2	
Table of Contents	4	
Chapter 1: General Introduction	6	
Part I	Posture studies	11
Chapter 2: Reorientation of a visually evoked postural response during passive whole body rotation.	12	
Chapter 3: Vection increases the magnitude and accuracy of visually evoked postural responses.	19	
Part II	Perceptual studies	24
Chapter 4: The influence of non-visual signals of walking on the perceived speed of optic-flow	25	
Chapter 5: Reduction of perceived visual speed during locomotor-type activity: Evidence for quadrupedal perceptual pathways in humans?	43	
Chapter 6: Reduction of perceived visual speed during walking: Selectivity for expanding optic flow components?	57	
Chapter 7: Summary and Conclusions	74	
References	77	
Appendix 1: The effect of stereoscopically and parallax defined scale on the strength of the arthrovisual effect	84	

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Declaration

The contents of this thesis are entirely my own work, with the exception of data collection for the attention-related section of chapter 4 and for chapter 5, which were done by my own student Miriam Berry as part of her degree project.

Adrian Thurrell

Introduction

Animals move around in their environment and almost all do so under their own control at least some of the time. In order to provide this control there must be an ability to detect and to sense, to a sufficient degree of accuracy, that animal's own self-motion. Humans may estimate their self-motion using a number of senses: hearing, vision, proprioception and the vestibular system. While all of these signal sources may be used to estimate self-motion, each subserves a different primary function, with consequent limitations. Hearing is primarily used to determine the presence, identity and position of noisy objects in the environment (whether generating, or reflecting sounds from another source). If such an object is stationary, its motion signal relative to an observer also determines the observer's self-motion. However, hearing cannot be used in the absence of sound, has poor localisation (when compared to vision) and only provides a motion signal of the head relative to the object. Vision also is primarily used to determine the presence, identity and position of illuminated objects in the environment. Again, the relative position signal of a stationary object may be used to determine the observer's self-motion. Vision, however, cannot be used in darkness, may be impaired by occlusions and again provides only a relative motion signal between the object viewed and the retinae, which are themselves mobile relative to the subject. The proprioceptive and somatosensory systems are able to signal the relative motion between the body and an object that it is in direct contact with. If this object is stationary, e.g. the ground underfoot, then a signal of self-motion may be obtained from this relative motion signal. This method relies on the stationarity of the contacted object, and that this contact is maintained. The vestibular system (and other possible gravito-inertial systems) provides a signal of changes in self-motion that is free from prior assumptions about the environment and functions continuously. However, excepting the response of the otoliths to tilt relative to gravity, the response to low frequency changes of motion is limited or absent making vestibularly derived signals of self-motion unreliable under certain conditions. Apart from the last, these signals of self-motion are relative to objects in the environment, which when in motion themselves will reduce the accuracy of the signal. To overcome the individual limitations of these signals of self-motion in all situations they must be combined effectively. This thesis investigates aspects of this combination of visual, proprioceptive, somatosensory and vestibular signals by

measuring the resultant self-motion signal under those conditions in which it is inaccurate.

Chapters 2 and 3 use postural control predominantly as a tool to investigate internal signals of self-motion. These chapters are concerned with the combination of retinal information with signals indicating gaze direction relative to the body in the visual control of posture (the position and motion of the centre of mass of the body relative to the feet on a supporting surface - see below). Chapters 4, 5 and 6 use the perception of visual motion speed as a tool to investigate self-motion signals arising from the proprioceptive system. In chapter 4 the use of locomotor signals to indicate self-motion in a manner that affects visual perception is established. In chapter 5, alternative motor activities are compared, showing a tuning for the similarity of the motor activity to walking in the use of proprioception to signal self-motion. In Chapter 6, the directional specificity of the walking derived self-motion signal is investigated using changes in the visual motion stimulus.

One means of measuring the self-motion signal is via postural sway: upright stance in humans is not passively stable and the postural system must therefore constantly control the postural muscles in reaction to current body position and motion. The penalties for an incorrect self-motion signal are high, e.g. falling-over, and the postural system may therefore be expected to accurately correct for any perceived deviation from the ideal position. For example, if a person has signals of self-motion as if falling or leaning too far to the right, their postural response will be to rapidly sway leftwards. When such a person's self-motion signals are accurate (i.e. they are leaning too far to the right) this will cause them to decrease their inclination from the vertical until they are once-again standing upright. However, if this person's signals of self-motion are inaccurate (i.e. they are actually upright), for example if their visual system has been tricked by a manipulation of the sensed environment, then their 'corrective' response will in fact take them away from upright stance and cause them to lean leftwards. We can then measure both the direction and the size of the inaccurate self-motion signal as of equal magnitude, but opposite direction to the resultant postural sway (Dichgans et al. 1975).

Vision provides motion signals relative to the retinae, and vestibular signals are relative to the head, both of which may rotate relative to the body. The influences of vestibular (Lund and Broberg, 1983) and visual motion (Wolsley et al. 1996) stimuli on postural control have been investigated with the head and/or the eyes rotated relative to the

trunk. In both these studies the postural response was always aligned to the direction of the stimulus, i.e. the response was reoriented in body-centric co-ordinates in order to take into account the head and/or eye rotations. In the case of Wolsley et al. (1996) a small portion of the visual field contained static reference points and the environmental structure was known, these cues may have helped the subjects reorient their sway cognitively. In chapter 2 therefore, a modified version of their method was used, taking place in the dark to remove background vision, and in which the environment was restructured, also in the dark, to reduce cognitive cues. This is proposed to test whether efference copy of neck muscle commands (considered to be a copy of the efferent muscle commands that is retained within the CNS, e.g. for use in predicting the outcome of actions before direct feedback is available) and/or proprioception are sufficient to mediate this reorientation of visual signals of self-motion from retino-centric into body-centric co-ordinates.

The visual stimulus used in chapter 2, consisting of a large rotating disk (the same as Wolsley et al.'s), is also able to elicit a conscious sensation of self-motion (vection) in the opposite direction to its own motion. This vection sensation alternates with periods during which no self-motion is consciously perceived, but only motion of the disk (object-motion perception). The visual motion induces postural sway during both vection and object-motion perceptual states, however, the induced sway is greater in magnitude during periods of vection (Kuno et al. 1999). Presumably, sensations of vection indicate signals of self-motion at a cortical level and this may provide an extra site for interaction between gaze direction and retinal signals to provide an accurate visual signal of self-motion. Therefore it would be expected that this reorientation would be more accurate during vection, when cortical signals are in agreement with those responsible for the postural response during object-motion perception. In chapter 3, the directional accuracy of the visually induced postural sway relative to the direction of the inducing visual motion was investigated during these two perceptual states.

Vision is primarily an exteroceptive sense (and also hearing and touch, though they are not considered further here), being used to estimate the motion of other objects in space, as well as providing a signal of self-motion (Gibson 1950, 1954, 1966, see also chapter 2). By its very nature, vision provides motion signals relative to the eyes, and therefore when the eyes are in motion vision alone cannot directly signal object-motion in space. However, our eyes are rarely stationary and yet common observation shows we are still

able to visually judge the motion of objects in space when the eyes are in motion (though probably with less accuracy). During eye motion, object-motion in space can be reconstructed as the vector sum of object-motion relative to the eyes (the retinal signal) and eye motion in space, therefore visual judgements of object-motion in space during eye motion depend on a signal of that eye motion. If 'perceived object motion' = 'the retinal signal' + 'the eye motion signal', then 'the eye motion signal' = 'perceived object motion' - 'the retinal signal'. During a constant (i.e. known) visual motion stimulus, object-motion perception may therefore be used experimentally as an indirect measure of the eye motion signal (Wertheim, 1994). This eye motion signal, may be composed of combinations of proprioception, efference copy, vestibular signals and vision as shown in the framework presented in chapter 4. While proprioceptive signals from the legs and efference copy of leg muscle commands have been studied in the control of posture they have received little attention from the perspective of visual processing.

Walking on a treadmill while viewing an artificially generated motion scene allows manipulation of efference copy and proprioceptive signals without concomitant changes in other sensory modalities by selectively de-coupling the normal dependency of visual flow on walking speed. By comparing the perception of the (constant) speed of motion of a large visual target during treadmill walking at different speeds the influence of these efference copy and proprioceptive signals of walking on vision can be measured. In chapter 4, an experiment is presented using this technique, demonstrating a reduction in the perceived visual speed of a constant speed target during walking, and that this reduction in perceived visual speed increases linearly with increasing walking speed. Two variations of this experiment are presented that serve to show that this effect is not caused by changes in attentional load (see Sahraie et al. 2001) or vestibular signals (see Probst et al. 1986), i.e. that leg proprioceptive and re-afferent signals are most likely to be responsible. A third variation shows that these signals directly influence motion perception without influencing timing perception. It is proposed that efference copy and leg proprioceptive signals provide a signal of self-motion that the visual system then uses in order to maintain perceptual constancy.

Motor activities other than walking may also provide signals of self-motion e.g. arm movements (Bles et al. 1995). However, it is expected that as the correlation between the type of movement and self-motion decreases, the strength of this effect should also reduce, several activities were therefore tested: walking, cycling, arm pedalling and

finger-tapping. Walking is an ideal provider of proprioceptive and re-afferent signals indicating self-motion: there is a direct link between the subject and the ground surface; it provides a direction as well as a speed signal; it is well practised throughout life and has a high correlation with self-motion. Upright walking, a quintessentially hominid activity, is also already known to have selective adaptive links to vision, that can lead to conscious illusions from sensory conflicts (Pelah and Barlow, 1996). Cycling has some properties in common with walking. Notably it uses much of the same musculature and is, in the population studied (Cambridge undergraduates), reasonably well practised and provides a speed signal, though less direct than that from walking. Arm pedalling may mimic the swinging of the arms during walking, whilst Finger Tapping has no inherent correlation with locomotion. Using these activities, predictions that the proposed mechanism is tuned to locomotor-like movements of the limbs are investigated in chapter 5.

When walking forwards in a straight line through a stationary environment and looking in the direction of travel, objects in that environment will appear, relative to the subject, to move backwards. When projected from the three dimensional world onto the two dimensional retinae this results in a pattern (optic-flow) of expanding motion moving away from a point indicating the heading direction. This pattern of motion is the direct consequence of forward self-motion in a stationary environment and consequently its perception is predicted to be influenced most strongly by signals of forward self-motion. Other patterns of optic-flow that contain motion less likely to be a direct consequence of forward self-motion may be envisaged, such as vertical translation or rotation of the visual scene. These patterns of motion are consequently predicted to be less influenced by forward walking than expansion, and this prediction is investigated in chapter 6. Secondly, when the gaze direction is not parallel to the walking direction, for example when looking to the side, the visual motion on the retinae corresponding to forward walking is normally changed. Consequently, the optic-flow pattern predicted to be most influenced by walking speed is changed, in a manner proposed to be similar to that acting in the visual control of posture in chapters 2 and 3, and these changes are also investigated in chapter 6.

Part I

Postural Studies

Chapter 2

Reorientation of a visually evoked postural response during passive whole body rotation.

Abstract

Visually evoked postural responses (VEPR) to a roll-motion rotating disk were recorded from normal subjects (Ss) standing on a yaw axis motorised rotating platform. The disk was fluorescent so that Ss could be tested in an otherwise dark room. Movements of the head and centre of foot pressure were measured whilst Ss looked at the disk with eyes and head in the primary position and whilst the rotating platform moved the Ss randomly to 0, +/- 45 and +/- 90 deg angles from the visual stimulus. Ss were instructed to maintain fixation on the centre of the rotating disk but the amount of horizontal eye and head movement used was not specified. Platform rotational velocity was set near threshold values for perception of self-rotation (~2 deg/s) so that Ss would find it difficult to reconstruct the angle travelled. The data showed that the VEPR occurred in the plane of disk rotation, regardless of body position with respect to the disk, and despite the subjective spatial disorientation induced by the experiment. Averages of the response revealed a good match (gain = 0.95) between disk orientation and sway direction. The horizontal gaze deviation required to fixate the centre of the disk was largely achieved by head motion (head 95%, eye 5%). The results confirm previous results that VEPRs are reoriented according to horizontal gaze angle. In addition, we show that the postural reorientation is independent of cognitively or visually mediated knowledge of the geometry of the experimental conditions. In the current experiments, the main source of gaze position input required for VEPR reorientation was likely to be provided by neck afferents. The results support the notion that vision controls posture effectively at any gaze angle and that this is achieved by combining visual input with proprioceptively-mediated gaze-angle signals.

Introduction

Vision is used in conjunction with proprioceptive and vestibular signals for spatial orientation and balance control. If a subject, standing upright and looking straight ahead in a room, spontaneously starts to fall to the right, the optic flow will be to his/her left. The correct righting response for the subject in this case is to increase the pressure on

the right foot and decrease it on the left, such that the change in forces act to rotate the subject's body leftwards. The usual cause of large-field visual motion is the movement of the retina in space; therefore large-field motion is treated as if it was due to self-motion by the subject. If this retinal motion is simulated by a visual scene moving to the left when the subject is in fact upright, then the change in pressures at the feet will act to destabilise the subject to the left, i.e. in the same direction as the visual motion. The response to a large-field moving stimulus is therefore to sway in the same direction in space as the visual motion (Dichgans et al. 1975; Clément et al. 1985; Bronstein 1986).

A common feature of many previous experiments is the use of visual motion stimuli that are viewed by the subject looking straight ahead, i.e. with both the eyes centrally placed in the orbits and the head centrally placed on the shoulders (Dichgans et al. 1975; Clément et al. 1985; Bronstein 1986). However, Wolsley et al. (1996) investigated the effect of supplying identical retinal inputs with the eyes and head at different positions in the yaw plane. It was found that subjects (Ss) reoriented the main direction of sway, so as to match the direction of the visual stimulus, for a variety of combinations of head-on-trunk and eye-in-orbit positions. However, this experiment was run in a well-lit visual environment, with Ss instructed to position themselves actively. Thus Ss may have been able to determine their orientation, and that of the visual stimulus, visually and cognitively. Herewith, we examine whether accurate reorientation of VEPR still occurs during passive body rotation and with diminished visual/cognitive cues.

Methods

Eight normal Ss aged between 21 and 33 years of age were instructed to stand relaxed, with arms at their sides, fixating the centre of a visual display. The visual display consisted of a large disk of diameter 0.9 m positioned 40 cm from the subject's nasion at eye level, such that it covered a large area of the subject's visual field (97°). This disk was covered in randomly distributed fluorescent circles of 2 cm diameter with an average density of 320 m⁻² and could be rotated around the visual axis at an angular velocity of 40 deg/s either clockwise or anti-clockwise. Acceleration and deceleration of the disk took less than 2 s. The visual environment was otherwise dark.

The Ss stood on a posturography platform (internal malleoli 3 cm apart), which measured the position of the centre of foot pressure (COP) in the anterior-posterior and lateral directions. A 3-D magnetic search coil system (Polhemus 3space Fastrack)

measured head position in anterior-posterior, right-left directions and yaw. Horizontal DC electro-oculography was used to monitor that Ss fixated the centre of the disk and to reveal the relative extent of the head-on-trunk and eye-in-orbit rotations. The posturography platform was mounted on an externally controlled rotating platform moving smoothly about a vertical axis at 2 deg/s. This is near the reported values for perception of rotation (Hulk and Jongkees 1948, for review see Jongkees 1974); pilot studies indicated that most Ss could not perceive being rotated with eyes closed. Thus the visual stimulus could appear between -90 deg (left) and +90 deg (right) relative to the Ss' trunk mid-sagittal plane.

During a trial, each subject started facing the disk at one of five platform positions: -90, -45, 0, +45, +90 deg. The stimulus sequence was as follows (see Fig. 1 bottom panel): 1) Stationary platform, stationary disk (15s), 2) stationary platform, rotating disk (30s), 3) rotating platform, rotating disk (22.5-90s, depending on amplitude of platform rotation), 4) stationary platform, rotating disk (30s) and 5) stationary platform and disk (15s), these periods were contiguous. There were 40 different possible trials: two disk rotation directions vs. five positions for the start-point and four positions for the end-point of platform rotation. Each subject experienced ten different trials in a Latin-square paradigm, the first trial starting and the last trial ending with the disk straight ahead. Ss remained in the dark between trials to prevent use of visual cues to determine their orientation.

All signals were sampled at 125 Hz and analysed off-line. COP was arithmetically normalised to represent the signal given by a 70 kg mass. Five seconds of the onset response (average position between 25 and 30 s of disk rotation) were measured, relative to the average position during the 15 s before disk rotation. For the offset response, 1 s was measured (between 1-2 s after cessation of disk rotation), relative to the average position during the last 15 s of disk rotation. Based on these position measurements, the average orientation of the VEPR was then calculated for all Ss at each onset or offset condition, e.g. clockwise disk rotation at +45o platform position. In order to control for the effects of platform rotation in isolation, four Ss were rotated six times each between -45o and +45o and vice-versa at 2deg/s whilst fixating the stationary visual display. This control experiment showed that Ss' COP shifted by a mean of 1.05 cm, SD 0.88 cm in the direction of body rotation; due to the randomisation process for disk and platform rotational direction this bias would be cancelled out.

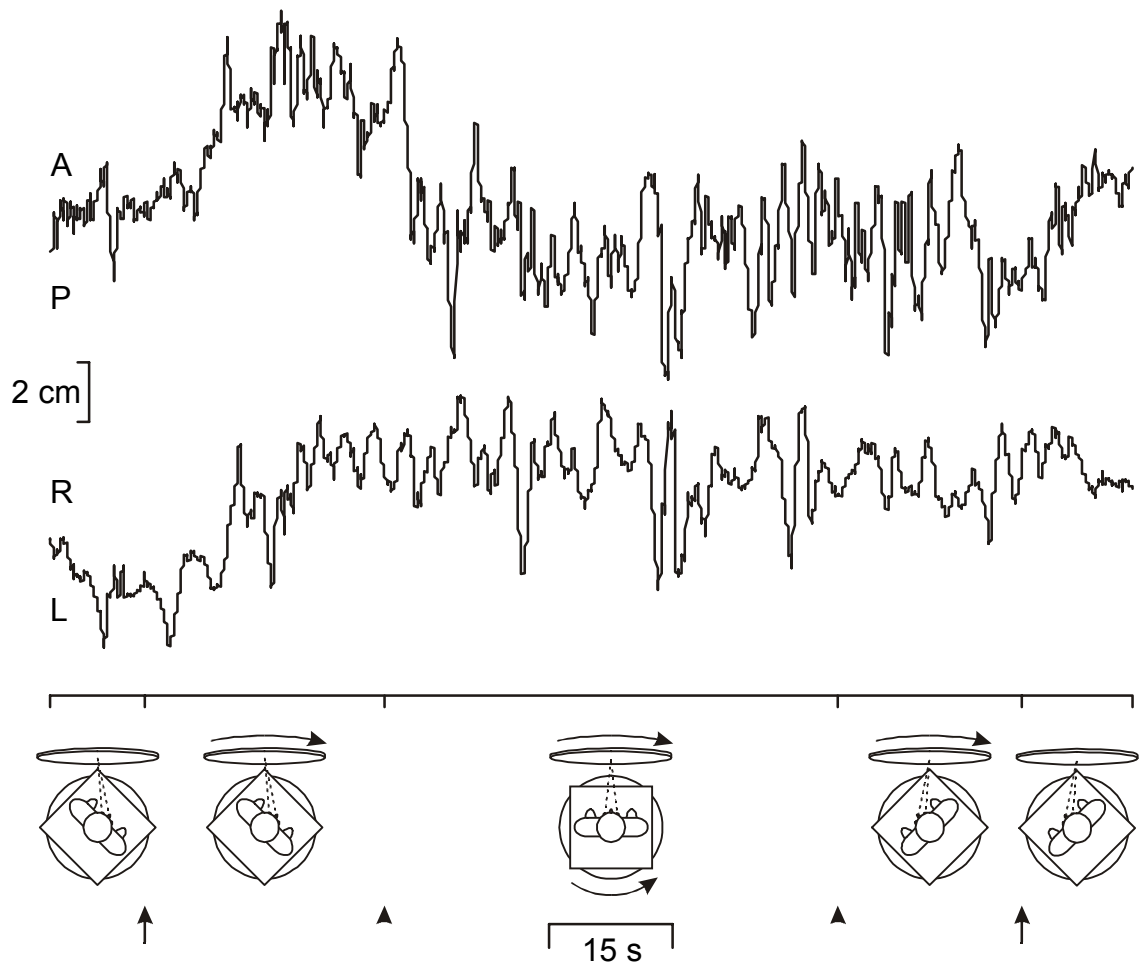


Fig.1 Raw platform traces from subject JB for the condition with clockwise disk rotation, starting condition at -45° (left) and ending at $+45^{\circ}$ (right) relative to the subject, the two traces show the anterior (A)-posterior (P) and right (R)-left (L) movements of the COP. The period of disk rotation is shown between the arrows and platform rotation between the arrowheads. The sequence of events is also represented by the icons below.

Results

Signals of head yaw and horizontal eye positions showed that the steady state reorientation of gaze for all Ss was mainly due to rotation of the head on the trunk (95%, SD 5%) with the remaining 5% performed by the eyes. During subject rotation, the proportion of movement carried out by the eyes sometimes exceeded this until further rotation of the head occurred. Subjectively, Ss were unsure of the relative position between themselves and the visual stimulus; some reported disorientation.

Figure 1 shows raw sway platform traces from one subject (JB) during the condition where the disk started at a position of -45° before moving (relative to the subject) to

+45°. The traces show the onset of the VEPR, with forwards and rightwards sway, at circa 25 s. As the platform rotates rightwards (between arrowheads, Fig 1) there is a reorientation of the COP from a right-anterior to a right-posterior position. On cessation of disk rotation (last arrow) the COP moves anteriorly and partly leftwards towards the original base-line position.

Visually evoked postural responses were normalised with respect to a 15 s period preceding the onset or offset of disk rotation. The orientation of the VEPR after 30 s (onset) or 1 s (offset) was converted into degrees relative to the Ss' trunk mid-sagittal plane for direct comparison with the orientation of the visual display. The reorientation of the VEPR at both the onset and offset of disk rotation, measured for COP signals for all conditions, is summarised graphically in Figure 2; a strong reorientation of VEPR by relative disk position can be seen. The best-fit curve reveals that the gain of the reorientation response at onset is ~ 0.82 ($y = 0.84x - 3.8$, $r^2 = 0.90$, as measured at the COP, and $y = 0.80x + 4.61$, $r^2 = 0.95$ measured at the level of the head; where x and y are visual motion and sway directions respectively). The offset response (at 1 s after the end of disk rotation) had a gain around unity ($y = 1.06x - 9.63$, $r^2 = 0.84$ as measured by the COP, or $y = 1.05x - 7.3$, $r^2 = 0.96$ as measured at the level of the head).

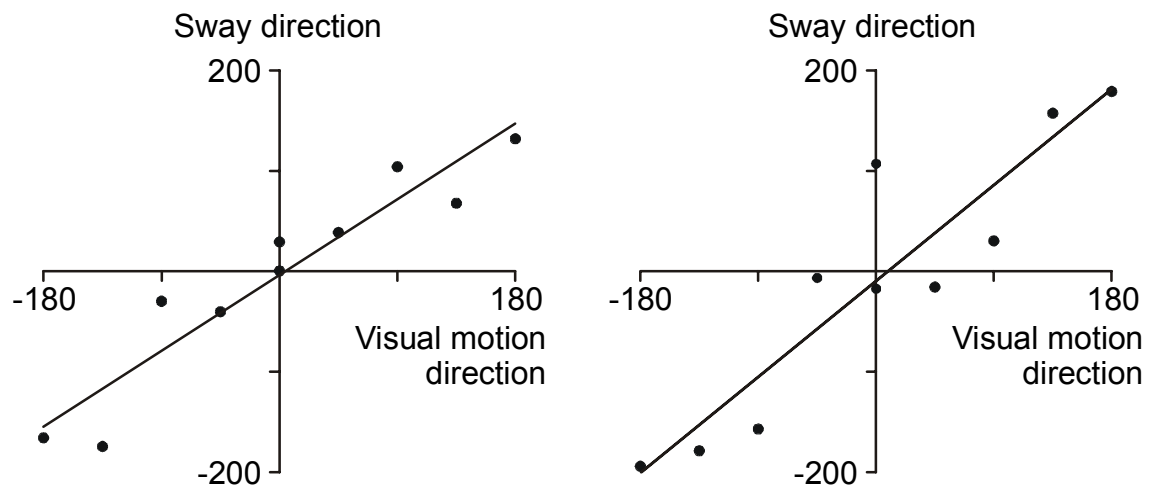


Fig. 2 Direction of sway (abscissa), as measured by the position of the COP, and line of best fit, plotted against direction of disk upper half motion, i.e. predicted sway direction (ordinate). Conditions were onset (left) and offset (right). All values in degrees, with zero corresponding to the direction of the subject's toes.

Discussion

Many previous studies have shown that visual motion is capable of generating postural reactions (e.g. Dichgans et al. 1975; Clément et al. 1985; Bronstein 1986), however, relatively few have investigated the influence of different positions of these stimuli relative to the subject (Stoffregen 1985; Gielen and Asten 1990; Wolsley et al 1996). Wolsley et al. (1996) reported an accurate reorientation of a VEPR during deviation of both the eyes in head and head on trunk. It was reasoned that, since the retinal motion stimulation was the same in the different positions, the postural reorientation must be due to eye-in-orbit and head-on-trunk position signals, possibly proprioceptive in origin. However, their experiment was conducted in a well-lit environment with Ss having prior cognitive knowledge of the position of the visual stimulus and of the relative rotations of the eyes and head. The present experiment was therefore conducted to test whether the reorientation of the VEPR is affected by reduced cognitive and background visual information and by passive positioning of the Ss with a rotating platform.

In the present experiment the directions of VEPRs induced by both the onset and offset of disk rotation were measured. The gain of the reorientation of VEPR was ~ 0.8 at the onset but ~ 1 during the offset. This slight difference may be explained by the fact that the posturally relevant sensory cues for vertical realignment of the body during disk rotation are conflicting, but those for realignment after disk rotation has ended are not. A comparison with the data of Wolsley et al. (1996) where they found a gain of reorientation of 1.08 ± 0.2 (calculated from published diagrams) suggests that little or no role is played by cognition, background visual structure or active positioning in the reorientation of VEPRs.

The origin of the signals used to determine the direction of gaze for visual control of posture is not yet clear. For the neck, proprioception would seem useful due to the possibility of external forces acting on the head. Neck afferents have been shown to be the main source of information used to estimate head-trunk horizontal angular deviation (Nakamura and Bronstein 1995). In the current experiments, where 95% of gaze deviation was achieved by head-on-trunk deviation, neck proprioceptive information is therefore the most likely source. Neck proprioceptive afferents are also thought to be responsible for the reorientation of vestibularly (galvanic) elicited sway during head turns (Lund and Broberg 1983; Britton et al 1993). External forces do not normally act on the eyes and, therefore, efference copy or a mixture of efference copy and ocular

proprioception has been favoured as source of an eye-in-orbit position signal. In pointing and estimation tasks (Bridgeman and Stark 1991) physiological gains of oculomotor efference copy and proprioception were found to be 0.61 and 0.26 respectively. The finding that extra-ocular muscle vibration elicits directional postural responses (Roll et al. 1989) suggests that at least some ocular proprioceptive component influences postural control. The current experiments suggest that visual and proprioceptive signals combine in order to provide effective, gaze angle-independent, visual control of posture. This process appears to be largely independent of cognitive comprehension of the geometry involved.

Chapter 3

Vection increases the magnitude and accuracy of visually evoked postural responses.

Abstract

Movement of large visual scenes induces an illusion of self-motion (vection) and postural responses. We investigated if the conscious perception of self-motion influences the magnitude and directional accuracy of visually evoked postural responses. Five normal subjects fixated the centre of a large disk rotating in the roll (coronal) plane. The disk was placed either in front of the subjects or obliquely 30deg to their right or left; in these oblique positions disk fixation was achieved by horizontal ocular deviation alone (i.e. no neck deviation). Subjects indicated their subjective perceptual status, either vection or object motion, with a push button. The results confirmed that the direction of the visually evoked postural response was reoriented according to the different eye-disk positions. In addition, both the magnitude of the postural response, and the accuracy of its alignment with the disk rotational plane, were significantly increased during vection periods. The results show that conscious perception of self-motion enhances visuo-postural performance. Since conscious perception is likely to arise at cortical levels, the findings indicate that the cortex is one of the sites where gaze direction interacts with retinal motion signals to provide a self-motion signal in body-centric co-ordinates. Such interaction provides a substrate for spatial representation during motion in the environment.

Introduction

Locomotor or postural movements create relative motion between the subject and the visual environment (optic-flow). Artificial full-field visual motion stimuli are often interpreted as due to self-motion and induce subconscious visually evoked postural responses and sometimes a conscious illusion of sensation of self-motion termed vection (Dichgans et al. 1972). At other times, however, perception is correct and the viewer reports that they are stationary and the disk is moving (object-motion perception). These two percepts comprise a bi-stable pair such that, when viewing a large rotating disk, there will be alternating periods of vection and of object-motion

perception. However, illusory signals of self-motion that may result in vection need not be consciously perceived to influence postural control under identical visual conditions (Previc and Mullen, 1991), and in fact, may have visuo-postural latencies many times shorter than vection (Clément et al 1983). However, a recent study found that postural sway during periods of vection was of a greater magnitude than during periods of object-motion perception (Kuno et al. 1999). Therefore, it could be expected that the induced postural sway during vection would become more accurately aligned with the moving visual stimulus. This would suggest, in turn, that conscious perception of self-motion improves visuo-postural control. These expected changes in the accuracy of orientation of the induced postural sway, comparing vection versus object-motion perception, were investigated here.

Methods

Five normal subjects between the ages of 21 and 31 were instructed to stand, relaxed, with their arms at their sides and their feet slightly splayed and separated upon a force platform. Subjects wore a light helmet carrying the receiver of a magnetic search coil system (Polhemus 3space Fastrack) measuring head position in all six degrees of freedom. Subsequent data processing was performed identically upon the horizontal position of the centre of foot pressure (COP) and on horizontal head position. In their right hand subjects held a button to indicate their perceptual state (vection or object-motion). All signals were recorded at 125Hz. In half the trials subjects were to press this button when they perceived themselves to be moving (i.e. vection) and in the other half only when they perceived the visual display to be moving (object-motion perception). The visual display consisted of a large (1.8m diameter, visual angle 122°) white disk, with a central fixation point, covered in smaller (5-20cm diameter) circles of various colours. This disk was rotated either clockwise or anti-clockwise at 50°/s and it was placed in one of three positions, either directly ahead of the subject or 30° to the left or right (see Figure 1a), all at 50cm from the subject's nasion. The centre of the disk was fixated with eye deviation only, i.e. no neck deviation, and viewed against normal laboratory lighting. Each subject was tested at each orientation with the disk always rotating clockwise or always anti-clockwise. Each trial lasted 300s with the disk being stationary for the first and last 10s, taking 7.5s to reach 50°/s and 5s to stop. The remainder formed a central period of constant speed disk rotation that was divided into perceptual periods determined by each subject's indication of vection or object-motion

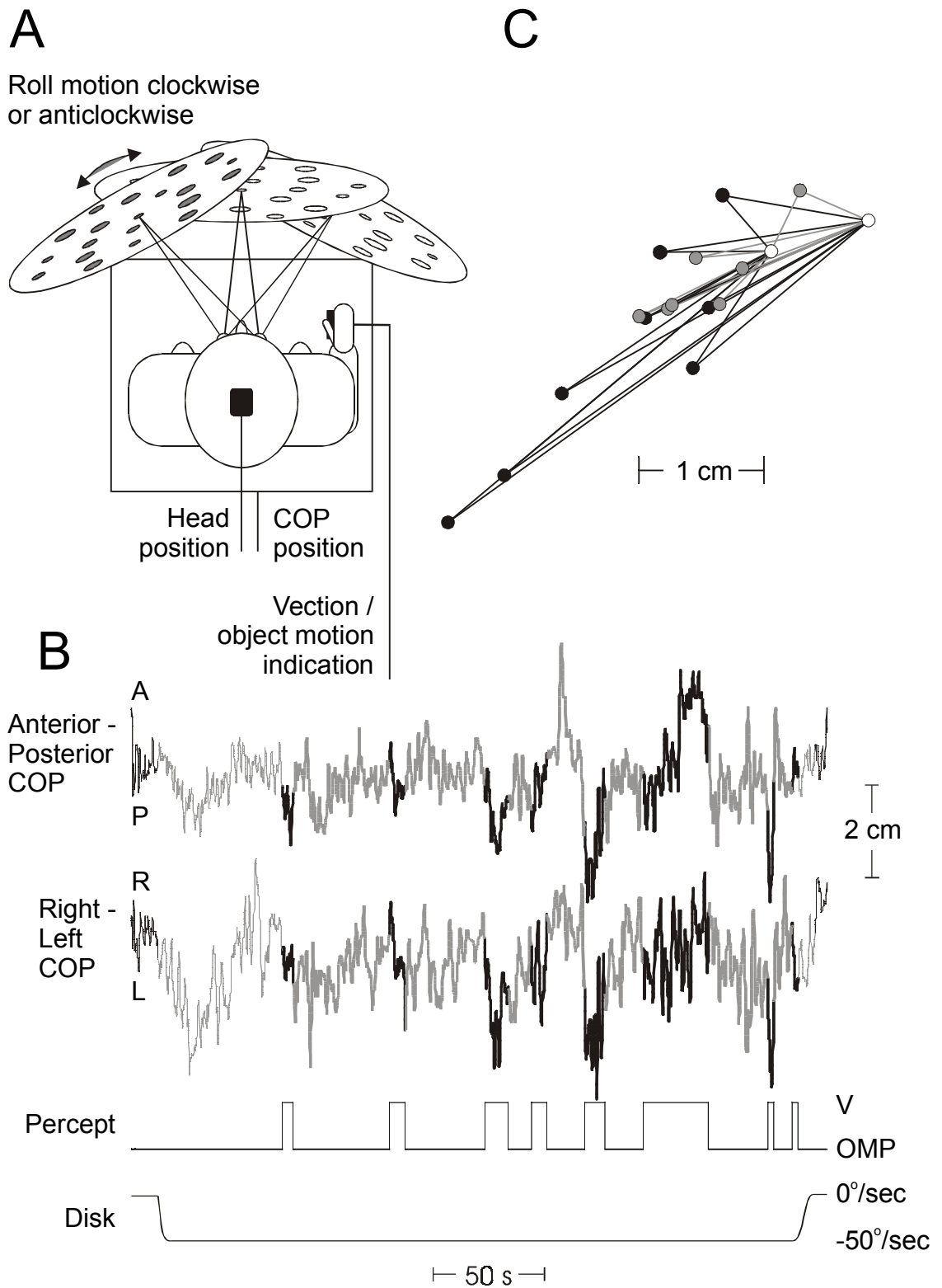
(see Figure 1b). Baseline positions were calculated as the means over the initial stationary period (0 - 10s) and the final 5s of the last stationary period. Sway (magnitude and the angular error relative to the orientation of disk motion) relative to both baseline positions were calculated during each perceptual period. Periods from the onset of disk rotation until the onset of the first vection percept and during the offset of disk rotation were discarded. The means of the sway magnitudes and direction errors across all periods for each perceptual state were calculated for each trial (see Figure 1c).

Results

The grand averages across all subjects and disk orientations of sway magnitude were calculated for each perceptual state (vection or object-motion perception). Sway deviation from baseline was found to be significantly greater ($P < 0.05$, paired t-test) during vection than during object-motion perception at both the level of the head ($5.8 \pm 0.56\text{mm}$ vs. $4.3 \pm 0.40\text{mm}$, mean \pm s.e.m.) and the COP (3.0 ± 0.39 mm vs. $1.7 \pm 0.19\text{mm}$).

Angular errors were also collapsed across subjects and disk orientations to reveal angular errors for each perceptual state (vection and object-motion perception). Comparison of the grand average of these errors revealed sway orientation to be significantly more accurate with respect to disk motion direction during periods of vection than during object-motion perception (32.60 ± 6.60 vs. 51.40 ± 7.90 , intersubject mean \pm s.e.m. direction error, at the level of the COP and 32.00 ± 6.70 vs. 40.50 ± 7.10 at the level of the head; $P < 0.05$, paired t-test).

Figure 1 Facing Page (A) The experimental set-up from above, showing the three disk positions relative to the subject. (B) Raw time signals from a typical trial (with the disk 30° left, rotating anticlockwise) showing periods of vection (thick, black lines) and object-motion perception (thick, grey lines) signalled by the subject to be compared to the baseline periods (thin, black lines). Intermediate periods during and immediately after start or cessation of disk rotation (thin, grey lines) are not used for analysis. (C) Data plotted showing the positions of sway during vection (black) and object motion perception (grey) and the trajectories from each of these positions to both baseline positions (white) from which the mean error direction for that trial was calculated.



Discussion

The results confirm data by Wolsley et al. (1996a) and Thurrell et al. (2000) showing that the direction of a visually evoked postural response tends to align with the plane of motion of the visual stimulus. Such re-alignment of retinal motion signals into body-centric co-ordinates by gaze direction, which may be mediated partly by proprioceptive

input from the neck and the extra-ocular muscles (Roll et al 1989; Wolsley et al 1996b), is critical in making visuo-postural control functionally useful in different directions of gaze. Also in agreement with a previous study (Kuno et al. 1999), is the greater magnitude of visually evoked postural sway during vection than during object-motion perception. The new result emerging from the current study is the finding of a more accurate alignment of visually evoked postural sway during vection than during object-motion perception. Since the perception of self-motion presumably arises at a cortical level, the implication is that the cerebral cortex is one of the sites where retinal motion signals are reoriented by gaze direction to allow for the visual control of self-motion. Indeed, neurones responsive to both retinal-flow and eye position have been found in areas MSTd (Bremmer et al. 1997) and 7a (Read and Siegel 1997), and our findings concur with the authors' claim that such cortical neurones could provide a substrate for spatial representation during motion in the environment.

Part II

Perceptual Studies

Chapter 4

The influence of non-visual signals of walking on the perceived speed of optic-flow

Abstract

To maximise the usefulness of information gathered about the environment, the visual system must be able to distinguish between retinal image motion that is due to object motion and that due to self-motion. During natural human locomotion optic-flow speed is determined by walking speed, consequently it is hypothesised that signals of self-motion may be used to discount the influence of self-motion on optic-flow. A number of signal sources or combinations thereof could be used to represent self-motion, e.g. vestibular, visual and locomotor (i.e. proprioception, somatosensation and efference copy). We considered how these non-visual signals of self-motion that accompany walking might influence the visual processing of optic-flow. In the experiments, subjects first viewed a constant velocity target optic-flow pattern while walking at one of a variety of speeds in a virtual reality locomotion simulator (Pelah et al, 1998). They were then required to match that perceived speed while standing still by adjustment of the scene velocity using a hand-held knob. The optic-flow pattern consisted of bright concentric rectangles, expanding and looming against a dark background, and viewed monocularly on a large rear-projected screen. Walking was found to directly influence perceived optic-flow speed (but not visually perceived timing) with increased walking speed decreasing the perceived optic-flow speed in a linear fashion. Perceived optic-flow speed was unaffected by attentional load or the head motion caused by walking. We suggest that perceived optic-flow velocity is modulated by non-visual signals of walking so as to discount the optic-flow arising from self-motion in order to reveal object motion in space.

Introduction

Accurate perception of the position of visual targets in space, and motion through it, has crucial survival advantages for many organisms, for instance for locating food, predators and for object recognition by means of perceptual grouping. However, for most organisms with vision, the eyes in space have six degrees of freedom: three of rotation (eyes within the head) and three of translation (eyes and head together), and

movement of the eyes along or around any axis has a profound effect on the images projected on the retinae. Thus, any determination of the position or movement of an object in the environment using the visual system must take account of the movements of the eyes in space. A somewhat simplified diagram of the inter-relationship of possible sources of information with which to accomplish this is shown in Figure 1.

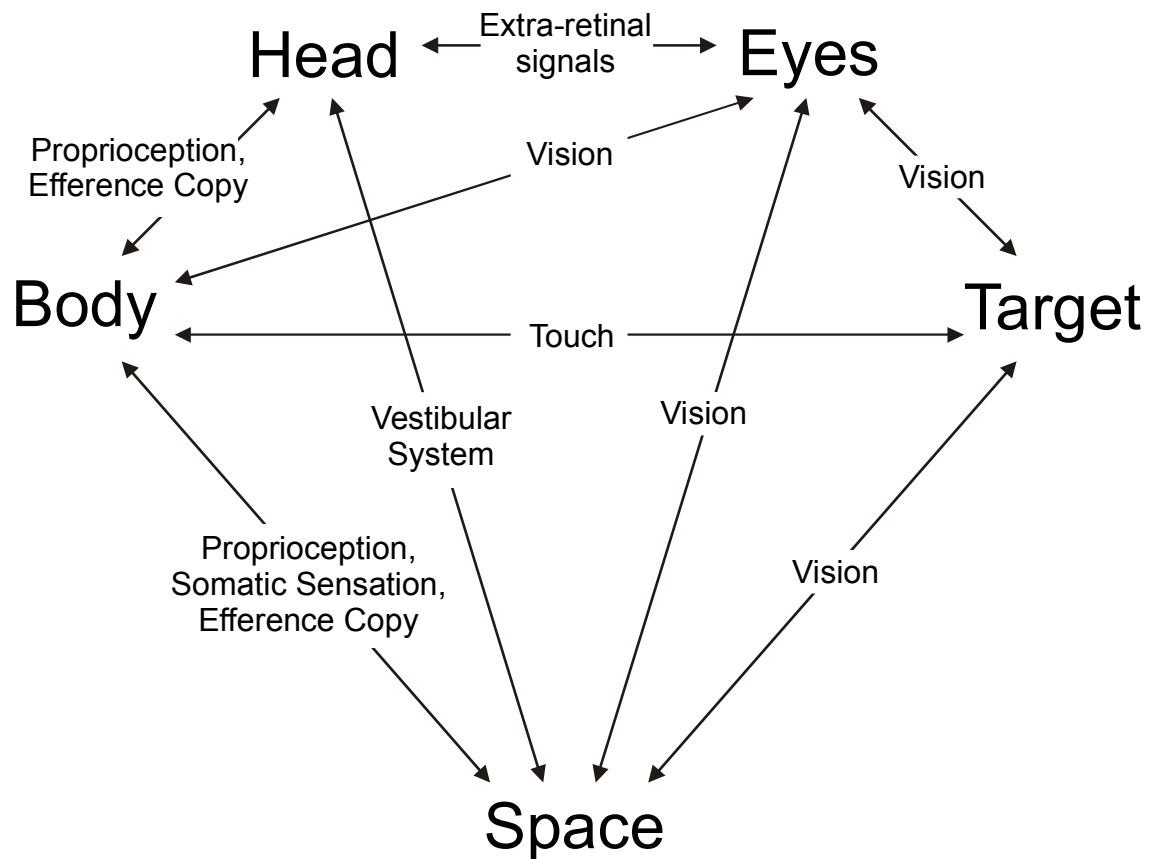


Figure 1 A simplified diagram of the connections between those body segments and portions of the environment that may be involved in the determination of Eye and Target motion. Some connections in the diagram correspond to a physical link, e.g. Head-Body, with information signalling their relative motion. Whereas others, e.g. Eye-Space, do not represent a physical link, but signals providing information about their inter-relationship are available. For convenience, the Body is treated as an amalgamation of the limbs and the trunk, and extra-retinal signals refer to both proprioception and efference copy for the eye muscles.

Retinal versus Extra-retinal signals of eye motion

Von Helmholtz (1896) was perhaps one of the first to consider this problem, in the context of rotational eye movements within an implicitly stationary head (i.e. the Head-Eyes-Target link of Figure 1). He concluded that the solution was to use signals of eye

movement and position from sources external to the eyes, i.e. proprioception from the extraocular muscles and/or efference copy of their commands, collectively referred to as extra-retinal signals. These extra-retinal signals would be used to remove changes in the retinal signal, (i.e. the signal travelling along the optic nerves) that are due to eye movements, and any remaining motion in the retinal signal could thus be treated as directly related to object position and movement in space. The alternative view to this, in its strictest form, originated with Gibson (1950, 1954, 1966), who concluded that all the necessary information about eye (as well as head and body) movements is contained in the visual image itself (the Eyes-Space connection of Figure 1). In this view, extra-retinal signals of eye position are, therefore, not needed to accurately determine object motion in space.

The importance or otherwise of extra-retinal signals in self-motion perception has been investigated in psychophysical studies on the visual perception of heading, the determination of the direction of self-motion. The perception of heading has been found to be equally effective with real and simulated eye movements, given equivalent visual information and under some conditions (Warren and Hannon 1988), suggesting that extra-retinal signals are not always needed. For simulating eye movements, fixating subjects are shown the motion that would have been perceived had the eyes been moving (which assumes, incidentally, that static extra-retinal signals for fixation are ignored, see Lappe et al. 1999). On the other hand, heading performance with simulated eye movements drops to chance levels when depth information is removed (Warren and Hannon 1988) and heading errors increase markedly with faster, more typical simulated eye movement velocities (Royden et al 1992), both supporting the use of extra-retinal signals. Also, that human subjects are capable of using retinal instead of extra-retinal signals to determine visual motion does not necessarily mean that they normally will. This ability seems to vary between subjects, with only some human observers able to determine heading direction during simulated eye movements without static depth cues (though dynamic depth cues were still present) (Stone and Perrone, 1997). On balance, it seems that a composite of the two signals is used that may be dynamically altered depending on their exact values, such as the non-linear combination shown by Brenner (1991), Brenner and van den Berg (1994), and Turano and Heidenreich (1996, 1999).

The nature of the extra-retinal signal

In order to account for percepts during visually induced sensations of self-motion (vection), a conceptual substitution is proposed for 'extra-retinal' (eye-in-head) signals by 'reference' (eye-in-space) signals (Wertheim 1994), made up of a combination of the former and also vestibular signals of head motion. This combined signal should therefore resolve not only eye- but also head-movements in judging self-motion. In support of this framework, perception of visual direction is indeed influenced by whole-body rotation in the dark (e.g. Blouin et al. 1998), and visual motion perception and the motion after-effect (Harris et al 1981) are both influenced by passive, whole-body linear movement (Pavard and Berthoz 1977, Buizza et al. 1980). Its weakness, however, is that the vestibular apparatus is unable to detect constant velocity motion, either linearly or rotationally, leaving a gap in signalling self-motion during these types of movement when the environment is not visible. A more complete reference signal of motion of the eyes in space would include not only self-motion signals from the vestibular apparatus, but also those from the other sensory modalities included in Figure 1.

Assuming a stationary torso, head-in-space signals could also be derived from a combination of efference copy and proprioception of the neck muscles. In avestibular patients, Mesland et al. (1996) showed the use of head-on-body signals in the perception of earth-relative object motion, while manipulation of neck proprioception was found to influence perception of visual targets in a manner indicative of their incorporation into signals of gaze direction (Biguer et al. 1988). Investigation of the interaction between efference copy, proprioception of the neck and vestibular signals showed perception was best explained by incorporating all three into the extra-retinal signal (Crowell et al. 1998), in a manner consistent with an extension to a reference signal of eye position in space (see Wertheim 1994).

The final link from eye to space from Figure 1 is between the body and space, as often the body is itself in motion and this must then also be taken into account. As it is rare (other than modern travelators and exercise treadmills) that we walk on moving surfaces, a natural alternative signal of self-motion would be that from locomotion. This combination of proprioceptive and somatosensory signals has been shown to enhance linear (Bles et al. 1995) and rotational (Jürgens et al. 1999) self-motion perception, influence ocular tracking (de Graaf et al. 1994) and modulate motion after-effects (Pelah and Barlow 1996, Pelah and Boddy 1998).

The current study

The simplest and perhaps most ecologically relevant locomotor stimulus is walking in a straight line, resulting visually in an expanding pattern of optic-flow for the observer. To test the hypothesis that proprioceptive and somatosensory signals of self-motion are incorporated into an eye-in-space reference signal, and consequently used to process the retinal signal, changes in visual processing were assessed at a number of walking speeds on a treadmill. Treadmill walking dissociates locomotor signals from actual self-motion (as well as other possible signals of self-motion using gravito-inertial cues). A visual matching task, between the perceived velocity of the same constant optic-flow stimulus during either walking or standing still isolated the effects of the locomotor signals. Having established the influence of walking upon perceived optic-flow velocity, various experiments were performed to determine its nature. These investigated the effect of differences in attentional load and head motion during walking, the influence of walking on temporal frequency (i.e. timing) perception, and the possibility that the influence is mediated as an after-effect.

Methods

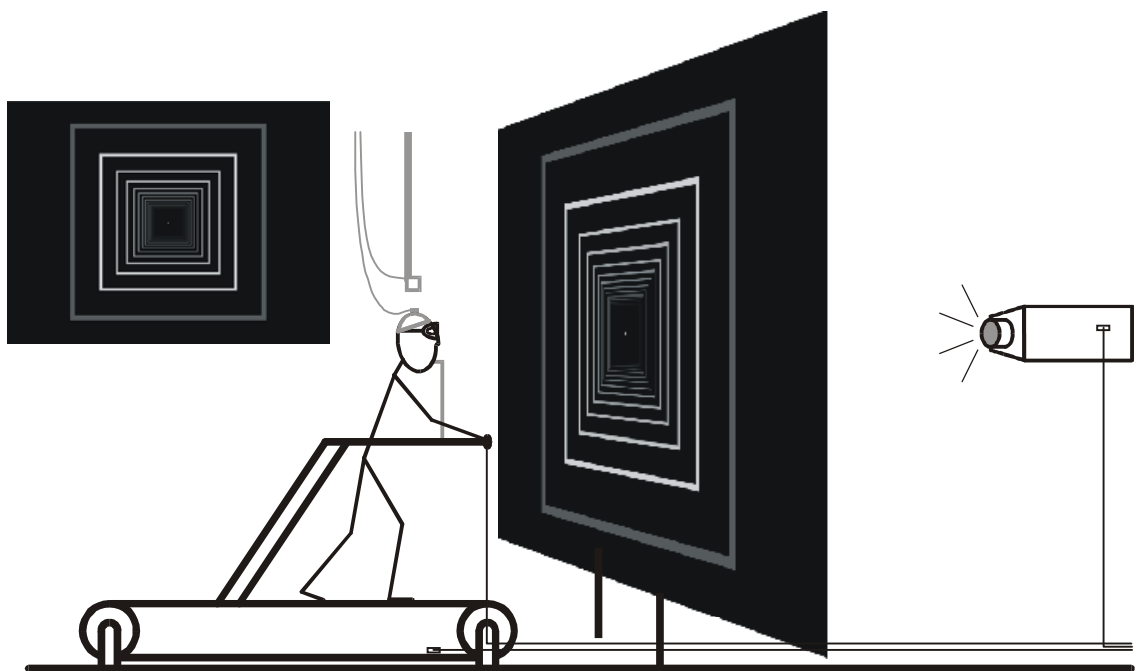


Figure 2 The general set-up and a screen-shot of the tunnel.

Subjects stood or walked upon an exercise treadmill (Woodway Exo 43) placed directly in front of a large rear projection screen (see Figure 2) based on the locomotion

simulator developed by Pelah et al. (1998). The treadmill was powered manually by the subjects pushing against the handrails with their arms, an action similar to (though less arduous than) pushing a trolley. The walking speed of the subject was obtained from a sensor attached to the treadmill axis, which was electronically low pass filtered and digitally sampled at 35Hz and then digitally low pass filtered at 8Hz to remove noise.

The image projected on the screen was contained within a central area 1.9m wide by 1.43m high and approximately 0.9m from the subjects' eyes giving a viewing angle of 93° by 77° . Subjects wore welder's goggles restricting peripheral vision and reducing brightness by a factor of 100, thus ensuring that the border of the screen remained invisible at all times. The goggles allowed only monocular vision, always with the right eye, removing stereoscopic depth cues. The visual scene was produced by an LCD projector (InFocus LP740) at a resolution of 1024 by 768 pixels and a refresh rate of 70Hz updated on alternate frames. The visual scene was composed of a simulated tunnel in depth (simulated relative dimensions, near-point relative to the observer = $0.4 \times$ width, far-point relative to the observer = $5 \times$ width, width = height) that consisted of 15 bright anti-aliased squares against a dark background (0.006 cdm^{-2}), as in Figure 2. The squares of the tunnel obeyed the laws of perspective, increasing in thickness and size with decreasing simulated distance to the observer, and luminosity changing as a trapezoid function of simulated distance (maximum luminosity 1.51 cdm^{-2}). This allowed fading of the rectangles into the distance with perspective and a reduction in brightness near the border of the screen, applied in order to remove flicker. A fixation point 1 pixel square ($0.12^\circ \times 0.12^\circ$, luminosity 1.51 cdm^{-2}) was also provided at the centre of the display approximately at each subject's eye level.

Subjects were required to perform a matching task between the perceived velocity of a 'target' visual motion scene and a number of 'test' scenes along the visual axis. These matches were made as a series of trials (see Figure 3): a 10s target presentation occurred during walking at one of six instructed speeds: 'stationary' (control), 'very slow', 'slow', 'normal', 'fast', or 'very fast,' and was followed by two stationary test presentations of 10s each. Instructions (presentation type and walking speed) were presented visually on the screen at the fixation point for 5s before each scene presentation. Subjects were instructed before each experiment to be walking at the instructed speed before the scene became visible and to adjust the test scene as quickly and accurately as possible to match only the most recent target speed. Each experiment

contained between five and twelve matches at each walking speed, resulting in a total session time of between 9 and 26 minutes.

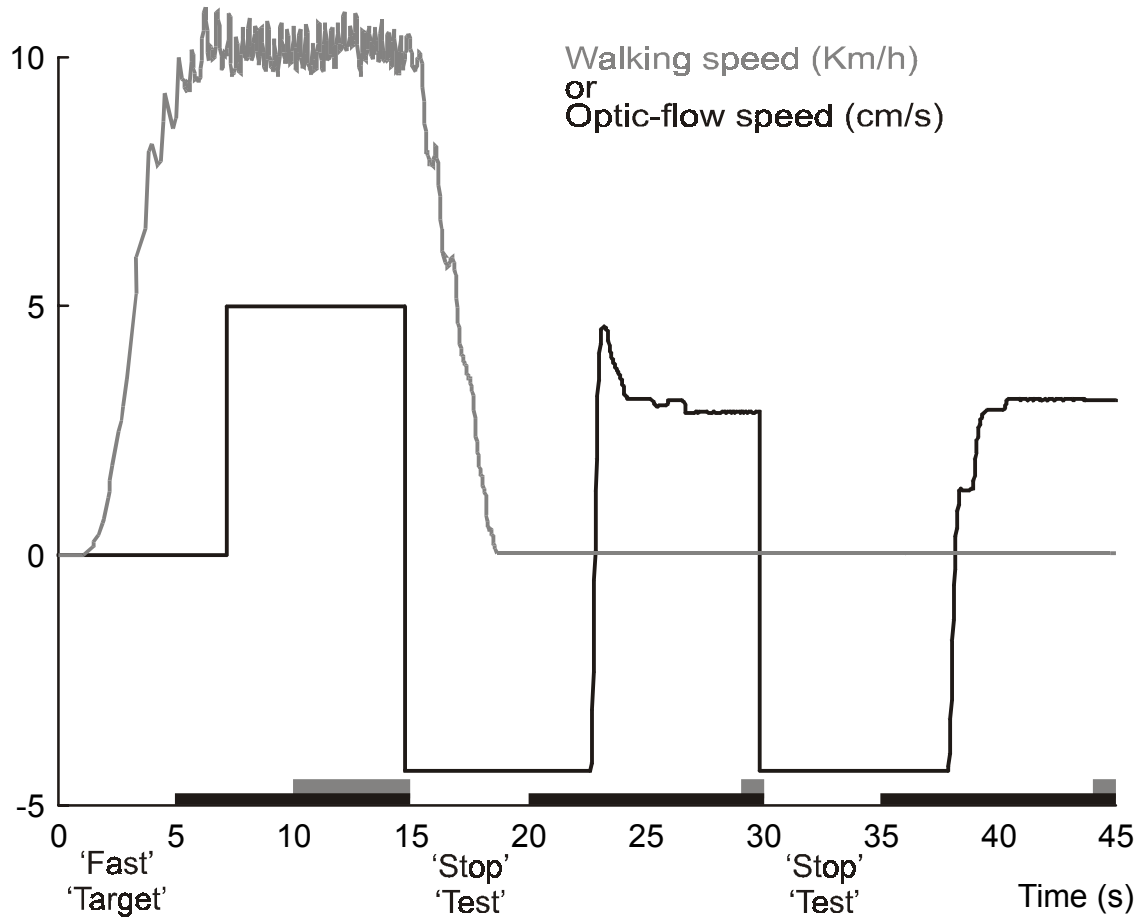


Figure 3 The time sequence of each trial. Instructions (printed below the time axis) were displayed for 5s each (thin portion of time-scale) alternating with the expanding tunnel (10s, thick portion). Mean settings during the last 1s (short grey bars) of each test tunnel were plotted against the mean activity speed during the last 5s (long grey bar) of the target tunnel.

The target velocity for the moving tunnel (expanding, simulating movement towards the subject) was always 5cm/s as measured by rectangle motion on the screen at the mid-hemifield position (27.8° from the fixation point, corresponding to 2.7°s^{-1} angular motion at the nodal point of each subject's eye). For the test presentations, the subjects used a rotating knob to control the velocity of the optic-flow tunnel. The knob was attached to the right handrail of the treadmill such that subjects could rest their hand at all times while making an adjustment. At the beginning of each matching presentation

the knob position was reset by the subject to a negative optic-flow velocity. The output of the knob was digitally sampled and low pass filtered at 35Hz and 8Hz respectively, and a small amount of noise added to the signal to mask the pixel jitter at low tunnel speeds. A small random offset was added to the knob position before each presentation to prevent subjects learning to use the knob position as a cue.

Data analysis occurred off-line with the walking velocity and visual velocity (or frequency in the case of the flicker stimulus) recorded and averaged over the final 5s and 1s of scene presentation respectively. A measure of setting accuracy was calculated as the standard deviation of the optic-flow velocity, and when this measure was over 0.5, suggesting the subject had not completed their adjustment, the trial was removed from further analysis. The order of presentation of conditions was randomised in all experiments. Prior to the beginning of trials subjects were allowed practice walking on the treadmill at the various instructed speeds, and matching the visual scene by adjusting the knob.

Variations

Four variations of the experimental method, for control purposes, were employed:

Reversal of walking condition between the target presentation and matching phases

In the main, type 1, protocol subjects viewed the target while walking and matched it while standing still. However, in this variant, referred to as type 2 trials, the target presentation occurred whilst subjects were stationary, with target matching taking place in six subsequent presentations of the test scene while walking, once at each speed. Matching during each of the six test scenes was to the target scene at the start of the block of presentations, i.e. that presented most recently. Type 2 trials control for the possibility that changes in matched optic-flow speed during type 1 trials are due to the act of walking distracting the subject from remembering the target speed. On the other hand, type 1 trials control for the possibility that changes in matched optic-flow speed during type 2 trials are due to the act of walking distracting the subject from setting the test speed.

An added attention test

The possibility that walking influences the matched optic-flow speeds because it is a competing load (see Wickens, 1980 for review) was investigated by adding an additional attention task. For trials with this added condition, during the 10s target

presentation while walking (i.e. type 1) subjects were instructed to listen through headphones to a pre-recorded series of five single digit numbers, and required to keep a running total which they were to call out immediately at the end of the presentation. Trials in which the subject miscalculated the total were discarded, as in such cases subjects may not have been sufficiently attentive.

Head stabilisation

During treadmill walking, the head may oscillate in all six degrees of freedom, which may be argued as influencing the perceived optic flow. Thus, some trials were conducted with restricted head motion, using a rigid bite-bar attached to the treadmill at an adjustable level for each subject, while remaining out of view. As an added test, head position was measured for one subject while walking using a Polhemus Fastrack magnetic position-sensing device, providing readings in all six degrees of freedom. The receiver of this device was attached to a light-weight helmet worn on the top of the head, mechanically independent of the bite bar (other than via the subject's head), with position data being collected at 35Hz. Head position was linearly detrended over the 10s of each trial during which the scene was visible and its FFT power spectrum calculated. These power spectra were averaged across condition repeats and walking speeds and compared. Linear motion was reduced by a factor of up to 15 laterally and up to 5 otherwise, whilst rotational motion was reduced by a factor of approximately 10 for yaw and roll, though pitch motion amplitude was unchanged.

Effects of walking on timing perception (flashing frequency)

Visual speed determination may, hypothetically, occur directly or as a construct of time and displacement, implying that walking may influence perceived optic-flow speed directly or through changes in temporal processing. Experiments to determine the influence of walking on temporal perception used a target consisting of an otherwise identical tunnel that remained stationary but flashed in place at a frequency of 2Hz. The tunnel luminance varied with a raised cosine profile applied to all tunnel components (i.e. rectangles) individually, such that their relative brightness remained constant (except for the fixation point, which did not flash). The flashing condition was compared to the influence of walking on perceived optic-flow speed by dividing each matched value by that of the target value to produce a normalised score.

Results

A number of control trials were conducted where no walking was involved, interspersed with the other experimental trials, and averaged as a measure of each subject's accuracy in matching a previously seen target velocity under the simplest viewing conditions. The conditions involved standing, for both target and matching presentations, while viewing the basic expanding tunnel stimulus (constant speed 5cm/s). Subjects individually had slight biases towards higher or lower matched velocities than the target value, but were generally consistent in their matches (see Figure 4).

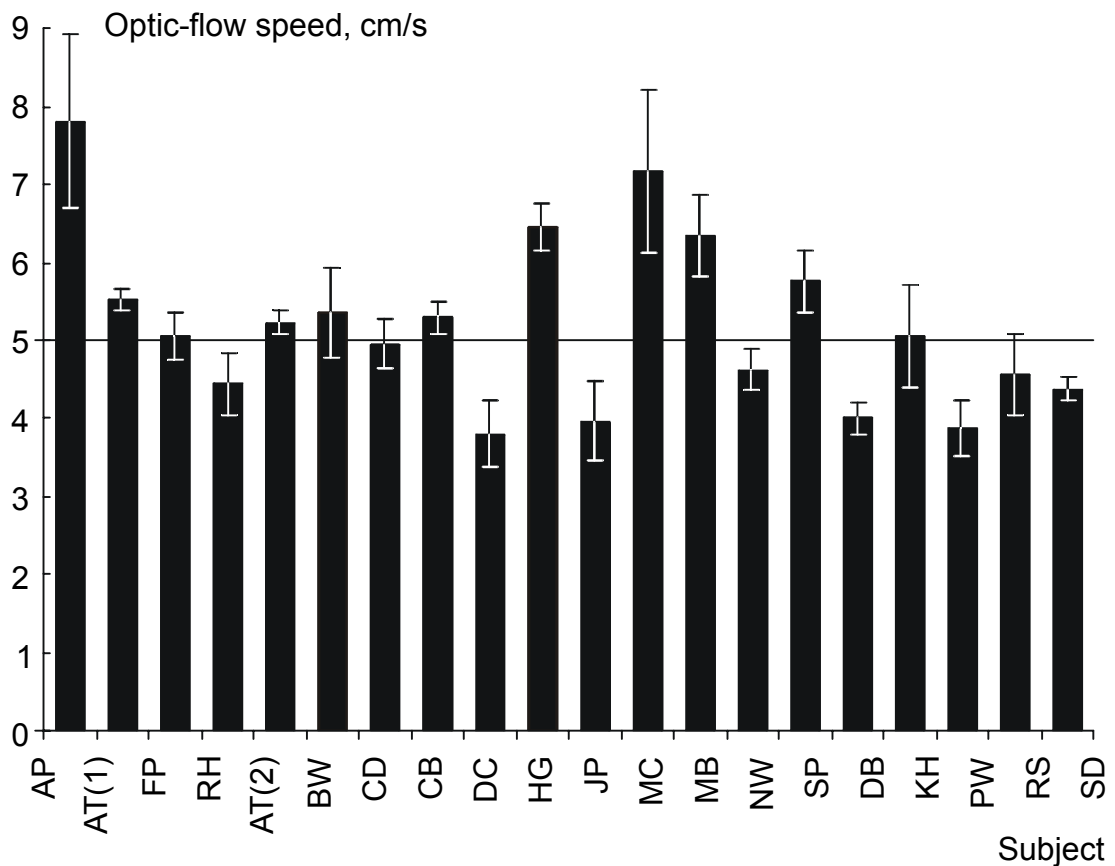


Figure 4 Mean (\pm s.e.m.) matched optic-flow velocity during the final 1s of each presentation (see Figure 3) for each subject during all trials. Some individual subject averages were significantly different from the target velocity of 5cm/s^{-1} , but the average of all subjects was not significantly different ($P > 0.05$).

Walking speed had a profound effect on the values matched by subjects to the constant target velocity. An example of the influence of walking speed on the perceived speed of tunnel expansion is shown in Figure 5. Approximately 70% (18 of 27) of subjects tested showed such a reduction of perceived optic-flow speed with increased walking velocity. The nine subjects who did not show a response were eliminated from the study. The

subject of Figure 5 represents a typical response pattern from the included group: as the subject walked faster during the target presentation, his matched speed settings were reduced. Matched speed settings are meant to indicate the subject's perceptually equal values to the constant optic-flow stimulus, implying that the target tunnel is perceived to be moving slower with increasing walking speed. All subjects, including naïve subjects who were unaware that the target speed was always the same, confirmed the observation verbally that the speed looks progressively slower while walking faster. The slope of the line of best fit can measure the strength of this effect, which for the subject in Figure 5 (CB) was -0.37 and significantly different from zero ($P < 10^{-14}$). The line of best fit intercepts the optical speed axis near the target speed of 5cm/s showing unbiased optic-flow perception during standing (cf. Figure 4).

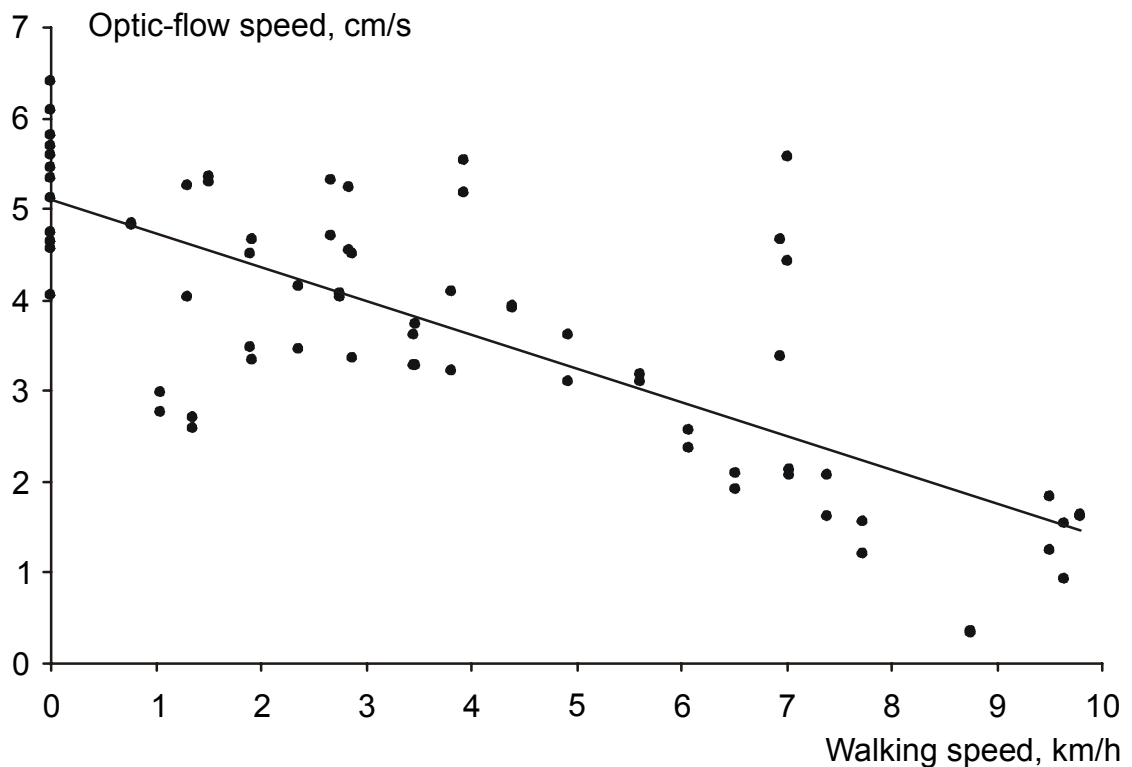


Figure 5 The main effect described here of increasing walking speed reducing the perceived speed of optic-flow. The similarity of the matched values to the target values when standing during both Target and Test can also be seen. The line of best fit had a Y intercept of 5.09, and a slope of -0.37 which was significantly different from zero ($P < 10^{-14}$).

It is possible that walking causes in some way a disruption of the subject's ability to remember the target optic flow velocity, so to test for this, complementary (type 2) experiments were conducted in which the order of events was altered. Target

presentation occurred during standing while matching occurred during walking, preventing any supposed disruption by walking of establishing a memory of the target velocity (see Methods). In the type 2 protocol, the slopes of the lines of best fit plotting optic-flow settings against walking speed were of opposite sign (as expected) and not significantly different in magnitude from the equivalent slopes for type 1 trials (Figure 6, Table 1).

Type 1 Trials		Type 2 Trials	
Subject	Slope	Subject	Slope
AT	-0.23	AP	0.55
BW	-0.91	AT	0.32
CD	-0.08	FP	0.81
CB	-0.37	RH	1.06
DC	-0.09		
DB	-0.46		
HG	-0.81		
JP	-0.37		
KH	-1.19		
MC	-0.59		
MB	-0.83		
NW	-0.25		
PW	-0.19		
RS	-0.34		
SP	-0.46		
SD	-0.29		
All	-0.47	All	0.68

Table 1 Slopes of best-fit lines for subjects used for either type 1 Trials or type 2 Trials. The average magnitudes of the slopes were not significantly different ($P > 0.05$).

	Control	Attention Task
AT	-0.23	-0.29
BW	-0.91	-0.49
CD	-0.08	-0.08
CB	-0.37	-0.49
DC	-0.09	-0.57
JP	-0.37	-0.39
MC	-0.59	-0.58
MB	-0.83	-0.10
NW	-0.25	-0.08
SP	-0.46	-0.45
All	-0.42	-0.35

Table 2 Comparison of slopes of lines of best fit during the standard control condition (type 1 trials) and the same experiment involving an additional attentional load (see main text). There was no significant difference in the mean slope magnitude. ($P > 0.05$)

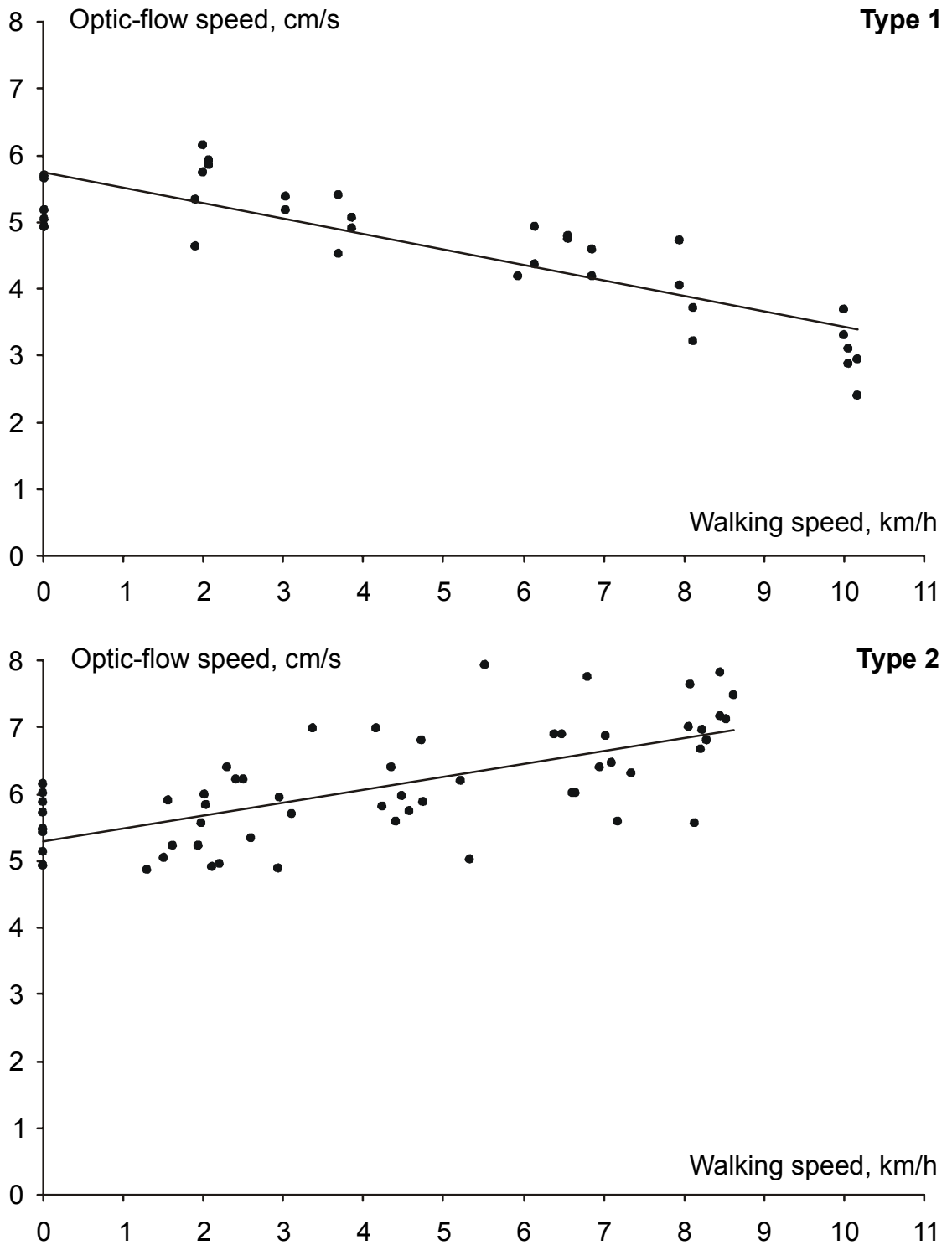


Figure 6 Data from subject AT for Type 1 and Type 2 trials, showing the slopes of best fit to be similar in magnitude but opposite in sign for the two presentation protocols. This reflects the influence of walking speed on the remembered target optic-flow speed or on the matched optic-flow speed respectively.

Changes in motion perception due to attentional load have been reported for first-order motion (Sahraie et al. 2001) and for motion after-effects (Chaudhuri 1990). To investigate the possibility that the influence of walking velocity on perceived optic-flow speed may be due to changes in attentional load, a comparison was made between performance with and without a concurrent numerical aural-verbal task. The strength of the effect (as measured by the slope of the best-fit line) during the attentional task was slightly lower than during control trials, though this difference was not significant (see Table 2), suggesting that cognitive overload was not responsible for the reported effect.

Movement of the head that results in vestibular stimulation causes an increase in visual motion detection thresholds and latencies (Probst et al. 1986) and there is, therefore, the possibility that the vestibular effect may extend as well to a reduction of supra-threshold perceived object motion speeds. When walking the head oscillates in all six degrees of freedom which, if this vestibular hypothesis is correct, may provide a mechanism for the described effect if the magnitude of the stimulation increased with walking speed. To determine whether head motion during walking indeed causes the observed changes in perceived optic-flow speed, some trials were conducted with restricted head motion. Using a bite bar rigidly attached to the treadmill, a comparison was made between treadmill walking with unrestricted or restricted head motion. Though the influence of walking speed on perceived optic-flow speed was on average lower during the reduced head motion condition (Table 3), this difference was not significant ($P > 0.05$). When comparing the amount of head motion between the conditions, the head was not held completely rigid, but that motion in all axes of freedom except for pitch was reduced by a factor of between 5 and 15. If the postulated mechanism were to predominantly work via pitch motion then little or no difference would be expected. However, this seems unlikely given that Probst et al. (1986) found significant effects on visual motion detection thresholds for yaw motion. Also rotations of the head in pitch and yaw have a similar influence on the retinal image they would be expected to have a similar influence on visual motion perception. The mechanism leading to reduced visual speed perception while walking cannot therefore be attributed principally to the vestibular system.

As discussed in the Introduction, there exists the possibility that walking affects not visual speed *per se* but rather timing, which could theoretically influence speed as one

of its constructs. The influence of walking speed on visual speed compared to temporal frequency perception revealed a significant difference (Table 4). The strength of the influence of walking speed on temporal frequency perception was not significantly different from zero ($P > 0.05$), combined with its significantly greater influence on optic-flow speed suggests that the latter could not occur solely as a consequence of a small effect on timing.

	Unrestricted	Restricted
AT	-0.23	-0.27
DC	-0.08	-0.01
HG	-0.64	-0.02
MC	-0.59	-0.26
MB	-0.82	-0.55
NW	-0.25	-0.28
All	-0.44	-0.23

Table 3 Comparison of slopes of lines of best fit during the standard control condition (type 1 trials) and the same experiment during which time the subject's head was steadied using a bite-bar mounted on the treadmill. No significant difference was found between conditions ($P > 0.05$).

	Moving	Flashing
DB	-0.46	-0.14
KH	-1.19	-0.20
PW	-0.19	-0.12
RS	-0.34	-0.02
SD	-0.29	-0.01
All	-0.50	-0.10

Table 4 Comparison of slopes of lines of best fit during matching optic-flow velocity and matching temporal frequency. To enable valid comparison, slopes are normalised for target speed and subject walking speed. The ratio of moving-to-flashing slopes was significantly different ($P < 0.05$) suggesting that the influence of walking speed on perceived optic-flow speed did not occur via changes in perceived timing.

Discussion

Subjects matched a constant optic-flow velocity lower during faster walking than slower walking, indicating that walking faster made the flow look slower, and did so consistently across subjects (Table 1, Type 1 trials). The display was monocular, and contained no familiar objects with an inherent scale, however a possible cue for scale is the symmetrical vertical structure of the tunnel: as the fixation-point at mid-height is

level with the subjects' eyes, the tunnel must be twice this height. This cue was subjectively weak, allowing subjects to interpret the scene alternatively as large, far away and moving quickly or small, close and moving more slowly (or perhaps something in between). Without robust depth cues, it cannot be determined whether the reduction in perceived optic-flow velocity is by an amount that would accurately compensate for the speed of walking. At the same time, however, the results are consistent with an hypothesis of perceptual constancy: that in this case the visual system uses efference copy and proprioceptive signals from the legs during walking to modulate the perceived velocity of optic-flow so as to establish the absolute velocity of objects in space. Comparison between subjects' matching during Type 1 and Type 2 trials revealed no difference in the size of the effect, but a reversal of its direction. This is consistent with signals of walking speed reducing perceived optic-flow speed only during walking, as part of a mechanism of perceptual constancy but not as an after-effect (since in Type 2 matching occurs during walking not after). A concurrent attentional task did not alter effect strength. Indeed, if attentional limitations were causing the effect then narrowing the cognitive bottleneck would be expected to heighten its influence not reduce it. Examining the head-stabilised data suggested that vestibular signals are not primarily responsible for the described effect. The slight reduction, however, could also be explained within the proposed context, as head oscillations are a normal component of walking and may combine with the complex of proprioceptive signals in judging walking speed to maintain perceptual constancy.

Neurons in primate dorsal medial superior temporal (MSTd) area have a number of the properties suitable for an area that supports the proposed visual constancy mechanism for self-motion. Most MSTd neurons have large receptive fields and are tuned to a continuum of first-order optic-flow motions (Graziano et al. 1994), making them ideal candidates for selecting self-motion from a complex motion stimulus. Many MSTd neurons, unlike MT neurons, also respond selectively to externally induced visual motion but not to motion induced by eye movements (Erickson and Their, 1991 and Bradley et al. 1996) or head rotations (Shenoy et al. 1999). Vestibular stimulation by linear whole-body movements also influences the direction selectivity of MST neurons in a manner that may disambiguate self- and object-motion (Duffy 1998, Bremmer et al. 1999). Signals of self-motion for MST neurons may arrive from the vestibular nucleus, a multi-sensory area whose neurons appear to encode self-motion whether derived from the vestibular apparatus (e.g. Daunton and Thomsen, 1979) or visually from large

field motion causing vection (Dichgans and Brandt, 1972). Proprioceptive signals of neck motion also play an important part in shaping the output of vestibular neurones (Gdowski and McCrea, 2000), whilst electrical stimulation of nerves in the limbs has been shown to affect the activity of vestibular nucleus neurones (Jian et al. 2002). The latter findings suggest that limb proprioceptive signals may be incorporated into signals of self-motion encoded by the vestibular nuclei, though this has not yet been confirmed electrophysiologically.

Since visual motion perception is thought to be correlated functionally, and in its neural locus, with visual motion adaptation leading to the motion after-effect (Tootell et al. 1995), the finding may also provide a mechanism for related findings. In the motion after-effect study of Pelah and Boddy (1998), it is possible that the reduction in perceived speed while walking resulted in less adaptation and therefore a weaker after-effect, compared to that perceived during standing. This would parallel the reduced motion after-effect reported when adaptation took place during passive vestibular stimulation (Harris et al. 1981), which may be explained similarly by a reduction in the perceived speed of visual motion during passive linear acceleration (Pavard and Berthoz, 1977).

An alternative (or additional) to this MST-vestibular nucleus locus of interaction between signals of locomotion and vision could be within the cerebellum. The cerebellum has been shown to have neurones responsive to large field motion (Fushiki et al. 1994) and also neurones involved in visual speed perception (Ivry and Diener, 1991), proposed to be dependent on mechanisms of timing perception based in the cerebellum (Ivry and Keele, 1989). This ‘time-space construct’ mechanism proposed for velocity representation in the cerebellum relies on stable representation of both time and space to function accurately, and changes in motion perception of a constant stimulus must be attributable to one or the other. In the current study, no subject reported any change in apparent dimensions of the tunnel with walking speed; therefore the ‘time-space construct’ mechanism would require changes in time perception alone, such as may be expected to co-vary with changes in cerebellar activity related to walking. There was no significant effect of walking velocity on timing perception (see Table 4), suggesting that the influence of walking speed on optic-flow perception does not occur in the cerebellum (or indeed elsewhere) via changes to a time-distance construct. Indeed, perception of velocity at higher walking speeds is such that the tunnel actually

appears stationary in some subjects, suggesting that velocity and position are quite separable, a finding which is difficult to reconcile with a ‘time-distance construct’ mechanism.

Conclusions

We present experimental results that reveal an important mechanism used by the visual system to maintain perceptual constancy during locomotion, achieved by the modulation of visual motion signals by signals representing walking along the same directional axis. This mechanism would form the end of a chain of signals expressing motion and position of the eyes relative to the head, to the body and to the ground (see Figure 1), and as such would provide a reference signal of eye motion in space (cf. Wertheim 1994). A number of specific predictions of this model may be tested experimentally: With specification of a real-world scale for the visual scene, perceived optic-flow speed should be reduced by an amount exactly equal to walking speed (see Appendix 1). There should also be tuning of the mechanism for the co-linearity of walking direction and optic-flow direction (see Chapter 6), for the optic-flow structure (see Chapter 6) and for the motor activity performed by the subjects (see Chapter 7). As there is no single method for reliable determination of self-motion and position in all circumstances, we suggest these signals of walking, in parallel and/or in series with other signals, as detailed in Figure 1, should allow robust, veridical perception of self- and consequently visual object motion in a wide variety of environments. However, as a consequence of this, there should also be a general caution when studying vision in isolation, as signals may be interpreted in vastly different ways depending upon the co-incident information from other modalities.

Chapter 5

Reduction of perceived visual speed during locomotor-type activity: Evidence for quadrupedal perceptual pathways in humans?

Abstract

When moving around, to maximise the usefulness of information gathered about the environment, the visual system must be able to distinguish between retinal image motion due to object motion from that due to self-motion. During walking, it has been shown that efference copy, proprioceptive and somatosensory signals may be used to reconstruct the speed of self-motion in humans (Thurrell et al. 1998). We considered how these signals might influence the visual processing of optic-flow during four motor activities containing progressively fewer elements similar to those present during natural locomotion, respectively, Walking, Cycling, Arm Pedalling and Finger Tapping. Subjects viewed an expanding optic-flow pattern, always moving at a constant target speed, while performing each of the above four motor activities at instructed speeds in a treadmill-based virtual reality simulator. They were then required to cease the motor activity and manually adjust, using a hand-held knob, the speed of a second, otherwise identical, test optic-flow pattern to match the previously viewed target pattern. The optic-flow pattern consisted of bright concentric rectangles, forming a tunnel, expanding and looming against a dark background, and viewed monocularly on a large screen. In agreement with previous findings, increasing walking speed resulted in a linearly decreasing perceived optic-flow speed for most subjects. As the motor activities became less similar to natural locomotion their influence upon optic-flow speed perception steadily reduced, with Finger Tapping not influencing optic-flow perception at all: Walking > Cycling > Arm Pedalling > Finger Tapping = 0. We propose that mechanisms responsible for the perception of optic-flow speed incorporate signals of self-motion from the limbs in order to discount visual distortions resulting from self-motion in proportion to the reliability of the movements of the limbs in signalling self-motion. In a further study, the direction of walking, i.e. forwards or backwards, was not found to affect the above mechanism: both faster forward walking and faster backward walking reduced the perceived speed of expanding optic-flow. This apparent lack of directional specificity may be a consequence of the incongruence between backward walking and expanding optic-flow.

Introduction

Accurate perception of the position and motion of visual targets in space has important survival advantages for many organisms: for locating food and predators and for object recognition via perceptual grouping. However, for most organisms with vision, the eyes in space have six degrees of freedom: three of rotation (mostly eyes within the head) and three of translation (mostly eyes and head together). Movement of the eyes along or around any axis has a profound effect on the images projected on the retinae; for example, during linear forward motion (along the line of sight) there results an apparent expansion of those objects along the direction of travel. Thus, any determination of the position or movement of an object in the environment using the visual system must take account of the movements of the eyes in space. A number of physiological sources, either individually, e.g. vision of the environment (Gibson 1950, 1954, 1966) or in combination, e.g. vestibular and extra-retinal signals together (Wertheim 1994) can signal the position and movements of the eyes in space (Figure 1). However, not all environments and situations allow all signals to be used, e.g. visual determination of eye motion cannot occur when the environment is dark, lacking in depth cues (Warren and Hannon 1988), or during fast eye movements (Royden et al 1992), and the vestibular system has a poor response to low frequency motion (Goldberg and Fernández, 1975). No single signal is accurate in all situations, so to enable robust determination of eye movements and hence visual perception, many signals must work in combination such that when conditions prevent one from providing useful information another may replace it.

A prominent cause of self-motion is walking, and during walking there are a number of additional signals that may be used to help determine self-motion through the environment: efference copy of muscle commands, proprioception and somatosensory signals. Signals arising from locomotion, unlike vision, are available in the dark, and unlike vestibular signals, are available during constant velocity motion. However, interpretation of locomotor signals relies on the assumption that the ground surface is stationary, an assumption seldom broken before the advent of modern travelers and exercise treadmills. By investigating visual perception during walking on an exercise treadmill, Thurrell et al. (1998) were able to show that such signals arising from locomotion are able to alter visual motion perception. Furthermore, such signals altered visual motion perception in a manner consistent with their use as signals of self-motion

by discounting those visual motion components (i.e. expansion) that would directly result from the walking speed indicated by the locomotor signals. This interaction between locomotor and visual signals was proposed to account for a visual motion after-effect resulting from a mismatch of visual motion and the locomotor signals from walking (Pelah and Barlow, 1996) that was suggested to result from the recalibration of sensory pathways by visuo-locomotor links.

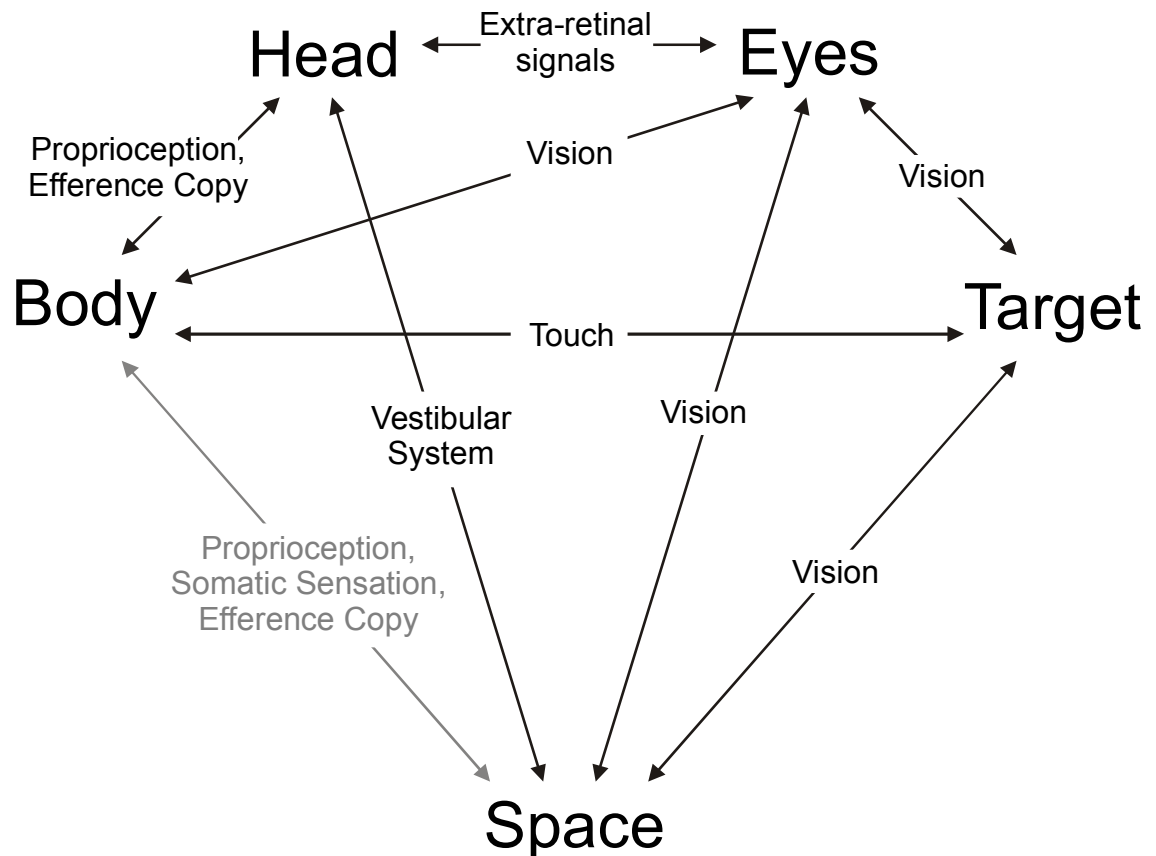


Figure 1 A simplified diagram of those body segments involved in the determination of target position and motion and the connections between them. Most, though not all, connections link to the target via the eye, requiring eye position to be accurately determined. Some connections correspond to a physical link, e.g. Head-Body, with the type of information signalling their relative motion, whilst others do not, e.g. Eye-Space, but about which signals of their inter-relationship are available. For convenience, the Body is taken as an amalgamation of the limbs and the trunk and extra-retinal signals refer to both proprioception and efference copy for the eye muscles.

Evidence that purely passive proprioceptive signals from the legs may dominate over vestibular signals in self-motion perception under some circumstances (Hlavacka et al. 1996) supports the use of locomotor signals to determine self-motion. However,

effeference copy and proprioceptive signals are not limited to the legs and such signals arising from arm movements have also been shown both to affect self-motion perception (Bles et al. 1995) and to enhance smooth pursuit tracking eye movements (de Graaf et al. 1994). The influence of efference copy and proprioceptive signals arising from the arms raises questions about the mechanism(s) involved in the use of such signals by the visual system. Might any movement of the limbs elicit changes in visual processing whether appropriate or not, or is there some specificity for the movement to be consistent with self-motion, i.e. is it only signals of limb movements that normally result in self-motion that alter visual processing? The mechanism hypothesised by Thurrell et al. (1998) predicts that limb movements correlated with self-motion would alter visual processing appropriately to discount the effects of that self-motion. Also, the strength of this alteration would be directly related to the degree of correlation between the limb movement and the self-motion. To determine whether this is the case, four activities sampling the range from natural locomotion to completely non-locomotor movements: Treadmill Walking, Stationary Cycling, Arm Pedalling and Finger Tapping were performed by subjects whilst they performed the same optic-flow matching task. A secondary investigation was also made into the direction of walking, the mechanism hypothesised by Thurrell et al. (1998) predicts that during backward walking, the expanding optic-flow pattern should be perceived as moving faster than when standing still, i.e. the opposite effect to walking forwards.

Methods

Subjects performed each of four activities: Treadmill Walking, Stationary Cycling, Arm Pedalling and Finger Tapping directly in front of a large rear projection screen (see Fig. 2). During Walking trials the treadmill (Woodway Exo 43) was powered by the subjects themselves pushing against the handrails with their arms, an action similar to (though less arduous than) pushing a shopping trolley. However, to ensure that this mimicked natural walking sufficiently accurately, a condition was added in which the treadmill was powered electronically by the experimenter and no walking speed instructions were presented to the subject (see below). No differences were found between optic-flow perception during electronically and manually powered walking, so only manually powered walking is considered further. Cycling trials were conducted using a stationary, recumbent exercise cycle (Tunturi Motivational Recumbent Cycle ECB F570), which was raised and altered to place the subjects' heads near to the position they maintained

during walking trials. Arm Pedalling was conducted using the exercise cycle, altered to allow the arms to rotate the pedals, and again keeping the subjects' heads in the same position as that during cycling. In order to reduce fatigue and to allow the subjects to reach their desired speed sufficiently quickly, the resistance was set to minimum for this condition. Finger Tapping trials were conducted while standing on the treadmill (with the belt locked), such that subjects' heads were in the same position as during walking trials and their hands were resting on the handrails of the treadmill. Finger Tapping involved all four fingers on each hand being moved together, alternating hands, with a button positioned under the left hand to record the tapping frequency. The Walking, Cycling and Arm Pedalling speeds of the subjects were obtained from sensors attached to the treadmill belt or to the spindle of the exercise cycle; these were electronically low pass filtered and digitally sampled at 30Hz and then digitally low pass filtered at 7Hz to remove noise.

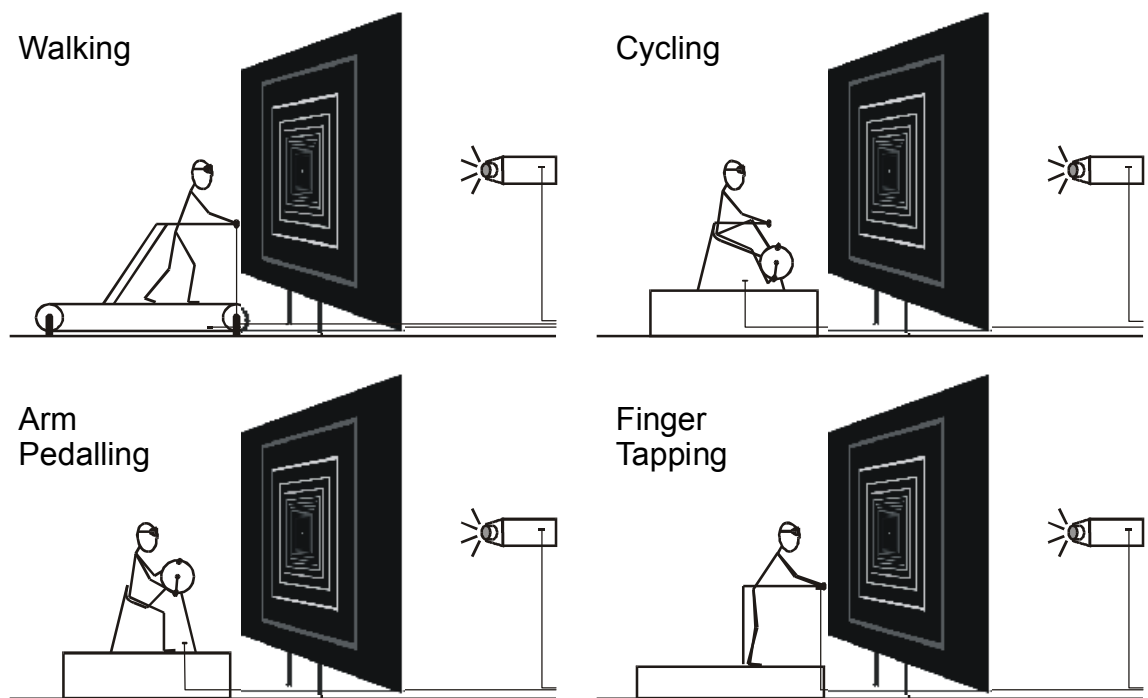


Figure 2 The experimental set-up for each activity.

The image projected on the screen was contained within a central area 1.9m wide by 1.52m high and during experimental trials it was approximately 0.9m (Walking, Finger Tapping) or 1.2m (Cycling, Arm Pedalling) from the subjects' eyes, subtending visual angles of 93° by 80° and 77° by 65° respectively. Subjects wore welders' goggles that restricted peripheral vision; thus ensuring that the border of the screen remained

invisible at all times. The goggles allowed only monocular vision, always with the right eye, removing stereoscopic depth cues and reducing the brightness of the image by a factor of approximately 100. Subjects were able to wear refracting spectacles inside the goggles if required, to correct their vision to normal. The visual scene was produced by an LCD projector (InFocus LP740) with a resolution of 1280 by 1024 pixels (single pixel visual angle was 0.09° or 0.07° at the central fixation point) and a screen refresh rate of 60Hz updated on alternate frames. The visual scene was composed of a simulated square tunnel in depth (simulated relative dimensions, near-point relative to the observer = $0.4 \times$ width, far-point relative to the observer = $5 \times$ width, width = height) that consisted of 15 bright squares against a dark background (0.006 cdm^{-2}), see Fig. 2. The squares obeyed laws of perspective: increasing in thickness and size with decreasing simulated distance and luminosity changing as a trapezoid function of simulated distance (maximum luminosity 1.51 cdm^{-2}). This allowed fading of the rectangles into the distance with perspective and a reduction in brightness of the closest squares near the border of the screen, this luminosity profile prevented flicker as squares came into, and went out of existence to maintain the constant length tunnel. A fixation point three pixels square ($0.28^\circ \times 0.28^\circ$, luminosity 1.51 cdm^{-2}) was also provided at the centre of the display approximately at each subject's eye level.

Subjects performed a matching task, made between the perceived velocity (along the visual axis) of a 'target' visual tunnel, and a number of 'test' tunnels. These matches were made as a series of trials (see Figure 3): a 10s target presentation occurred during walking at one of six instructed speeds: 'stationary' (control), 'very slow', 'slow', 'normal', 'fast', or 'very fast' and was followed by two stationary test presentations of 10s each. Instructions (presentation type and walking speed) were given visually at the fixation point for 5s before each scene presentation. Subjects were instructed to be at the required walking speed before the scene became visible and to match only the most recent target speed by adjusting the test scene as quickly and accurately as possible. Each experiment contained between five and twelve matches at each walking speed, resulting in a total experimental time of between 9 and 26 min.

The target velocity for the moving tunnel (expanding, simulating movement towards the subject) was always 5cm/s as measured by square motion on the screen at the mid-hemifield position (27.8° from the fixation point, corresponding to 2.7°s^{-1} angular motion at the nodal point of the subjects' eyes). For the test presentations, the subjects

used a rotating knob to control the velocity of the optic-flow tunnel, attached to the right handrail of the treadmill such that subjects could rest their hand at all times. At the beginning of each matching presentation the knob position was reset by the subject to a negative optic-flow velocity. The output of the knob was digitally sampled and low pass filtered at 30Hz and 7Hz respectively, and a small amount of noise added to the signal to hide the pixel jitter at low tunnel speeds. A small random offset was also added to the knob position for each presentation to prevent subjects using knob position as a cue.

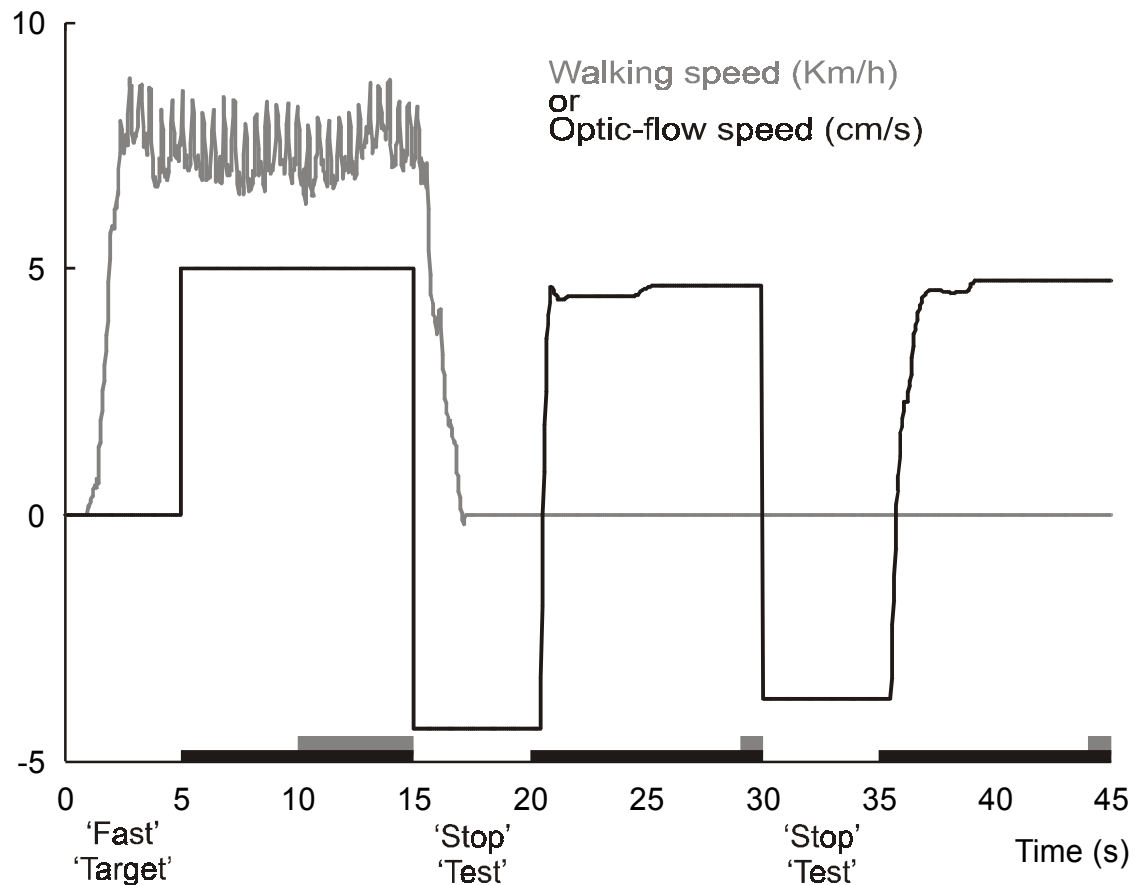


Figure 3 The time sequence of each trial. Instructions (printed below the time axis) were displayed for 5s each (thin portion of time-scale) alternating with the expanding tunnel (10s, thick portion). Mean settings during the last 1s (short grey bars) of each test tunnel were plotted against the mean activity speed during the last 5s (long grey bar) of the target tunnel.

Data analysis occurred off-line, with the mean activity speed and tunnel speed over the final 5s and 1s of scene presentation recorded respectively. Activity speeds were normalised as a proportion of the mean speed during the ‘very fast’ trials of that type. For walking trials, the stride frequency was also calculated as follows: walking speed

over the 10s of scene presentation was 4th order bandpass filtered between 0.75 - 9.0Hz and the power spectrum was then calculated using the Yule-Walker autoregressive algorithm (Marple, 1987). The modal frequency was then found and divided by two to convert step frequency into stride frequency and these values checked by eye in plots of walking speed against stride frequency to remove erroneous values. A measure of setting accuracy was calculated as the standard deviation of the test optic-flow velocity, and when this measure was over 0.5, suggesting the subject had not completed their adjustment, the trial was removed from further analysis. In all experiments, all conditions were randomly ordered. Subjects were given practice beforehand in Treadmill Walking, Stationary Cycling, Arm Pedalling and Finger Tapping at the various instructed speeds, and matching the visual scene by adjusting the knob.

To allow investigation into the influence of the direction of walking, a fifth motor activity was used in which subjects were required to walk backwards as well as forwards. Backwards walking conditions were conducted by adding two new walking speed instructions: 'slow back' and 'fast back', such that they were conducted as part of a longer trial involving walking both forwards and backwards, subjects were also given practice with these beforehand. In this variation, the order of events was reversed, referred to as 'Type 2' in chapter 5, such that target presentations occurred whilst subjects were stationary, with target matching taking place in eight subsequent presentations of the test scene, each while walking at one of the instructed speeds. Matching during each of the eight test scenes was to the target scene at the start of the block of presentations, i.e. to the target that was presented most recently.

Results

An example of the influence of walking speed (from the Treadmill Walking condition) on the perceived speed of optic-flow is shown in Figure 4. As walking speed increases during the target presentation, the target is perceived to be moving more slowly and consequently the matched optic-flow speeds are lower. Approximately 70% (16 of 24) of subjects tested showed a reduction of perceived optic-flow speed with increasing walking speed. The subjects who did not show a response may have misinterpreted the instructions, have become confused, or were not sufficiently immersed in the virtual environment and were thus eliminated from the study. The subject shown in Figure 4 shows a typical response from the included group: as the subject walks faster during the target presentation, the target tunnel is perceived to be moving slower, consequently

during the test presentations the matched optic-flow speed is set to this lower remembered value. The strength of this effect can be measured by the slope of the line of best fit, which for the subject shown was -4.04 and significantly different from zero ($P < 10^{-8}$). The line of best fit intercepts the optical speed axis near the target speed of 5cm/s indicating unbiased optic-flow perception when standing still.

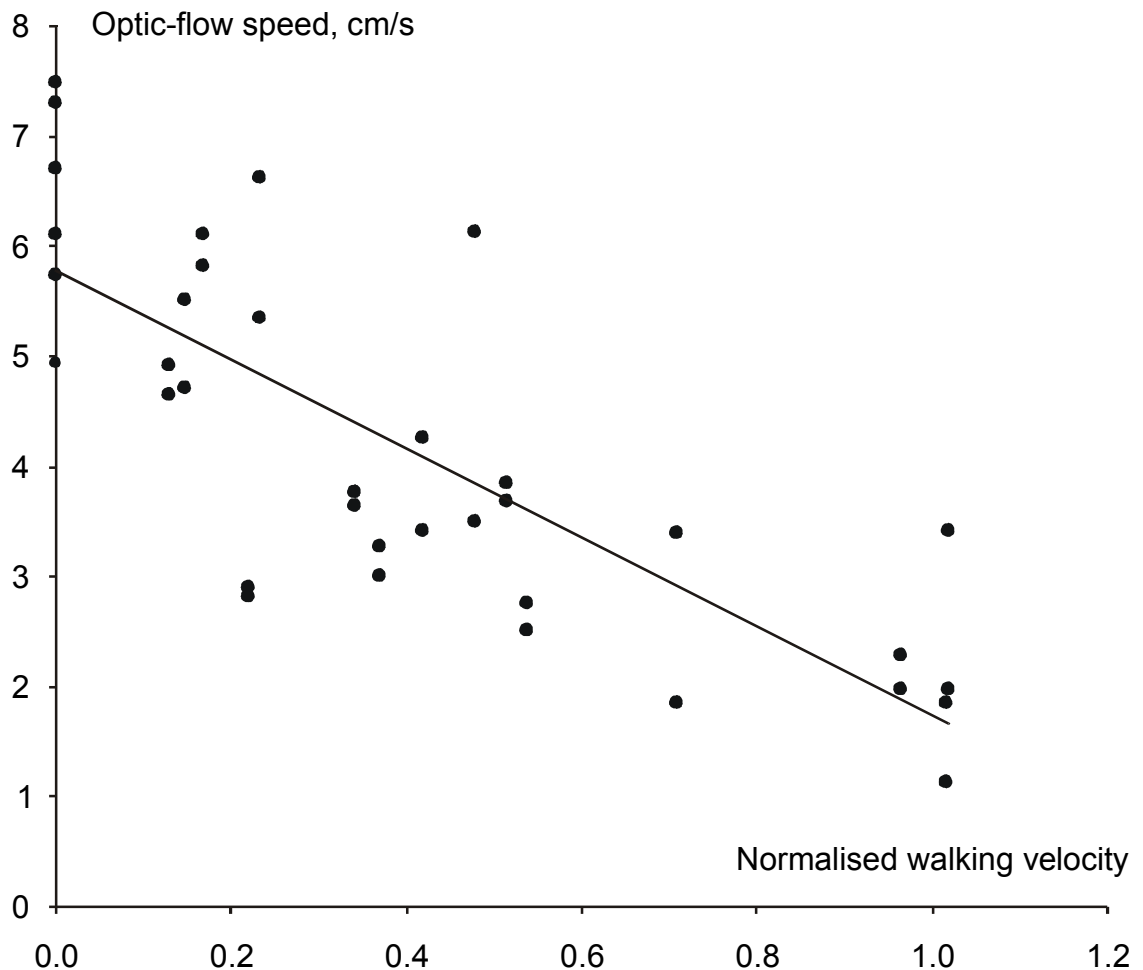


Figure 4 The basic effect of increasing walking speed reducing the perceived speed of optic-flow. The similarity of the matched values to the target values when standing during both target and test can be seen. The line of best fit for this subject (BW) had a Y intercept of 5.78 , and a slope of 4.04 which was significantly different from zero ($P < 10^{-8}$).

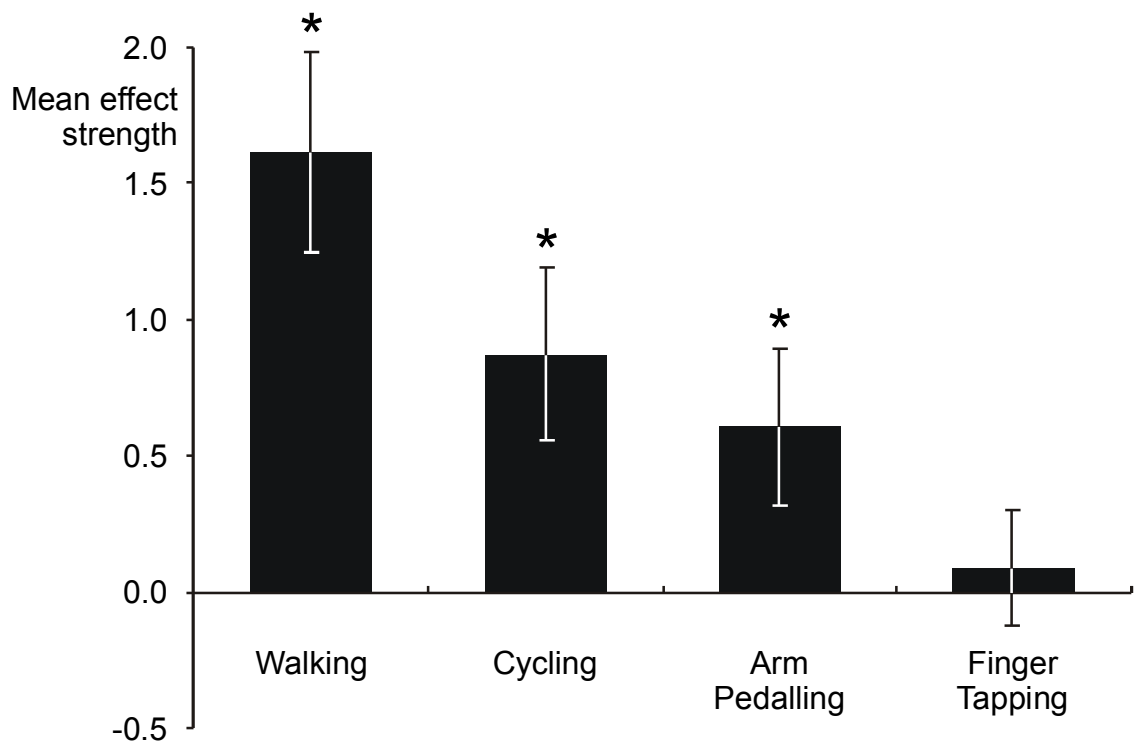
Motor Activities

To determine the types of motor activity than can affect the perception of optic-flow speed, subjects' visual motion perception was tested using all four motor activities under otherwise identical conditions, and the results are shown in Table 1. While walking is predominantly considered a translational process, with speed measured by distance

covered per unit time, it can also be considered as a cyclical activity with speed measured by stride frequency. Walking velocity and stride frequency are highly correlated, and no significant differences were found between these measures in terms of their influence on optic-flow speed perception; therefore stride frequency was used to allow direct comparison between all four motor activities. Cycling is a more ‘indirect’ activity than walking, in that there is not a one to one relationship between the speed achieved and either cadence or effort; cadence was used for comparability with other activities. Arm pedalling was conducted in the same manner as cycling and therefore the same considerations apply. Finger tapping has no inherent speed, as it is completely non-locomotor, so must be measured as a frequency of action. Differences in the natural rates of each type of action were removed by normalising to the mean of the fastest rates at which each subject performed. The comparison between the motor activities showed a trend from Walking through Cycling and Arm Pedalling to Finger Tapping in the strength of the influence of the motor activity on optic-flow speed perception (see Figure 5). Effect strengths for Walking, Cycling and Arm Pedalling were significantly different from zero, and effect strength for Walking was also significantly greater than for Cycling.

Subject	Treadmill Walking	Stationary Cycling	Arm Pedalling	Finger Tapping
AB	-0.08	0.24	1.57	1.03
BW	-4.04	-3.56	-1.02	-0.14
BD	-0.81	-0.45	-0.83	-0.10
CH	-0.16	1.60	0.11	0.06
EM	-2.33	-1.18	-0.45	-0.72
EW	-1.84	-1.35	-1.30	-0.07
HP	-1.15	-1.84	-0.73	0.66
JG	-2.40	-1.01	-0.93	0.31
KL	-0.59	-0.59	-2.85	-0.58
KR	-0.42	0.80	-0.16	0.54
LO	-2.80	-1.32	-0.27	-2.47
MN	-1.72	-1.04	-2.53	0.57
MH	-5.20	-2.85	-1.43	-1.00
PL	-0.03	-0.17	0.17	0.58
SM	-0.96	-0.68	-0.06	0.21
TR	-1.33	-0.61	1.04	-0.26
Mean	-1.62	-0.87	-0.61	-0.09
S.E.M.	0.37	0.31	0.28	0.21

Table 1 Slopes of best fit lines (effect strength) during all four locomotor activities for each subject.



*Figure 5 Intersubject mean (\pm s.e.m.) strength of effect as measured by absolute normalised slope, showing the trend in effect magnitude from walking to finger tapping. Effect strengths for Walking, Cycling and Arm Pedalling are all significantly different from zero ($P < 0.05$), but not for Finger Tapping. * Denotes a significant difference from zero.*

Walking Direction

Three subjects were used to compare walking forwards and backwards on perceived optic-flow speed. This investigation was conducted with a modified order of events in which subjects were stationary during the target presentation and walking during the matching presentations (type 2 trial, chapter 5). As walking speed increased it reduced the perceived optic-flow speed of the concurrently viewed scene (now the matching scene) therefore the matched optic-flow speeds are now higher than the target speed (see Figure 6). Best-fit slopes were of opposite sign, but otherwise similar to those found previously. During backward walking the more negative the walking speed, the greater the matched optic-flow speed, producing a line of best fit similar to that for forward walking but mirrored in the Y axis. This suggests that walking speed but not direction influences the processing of optic-flow speed.

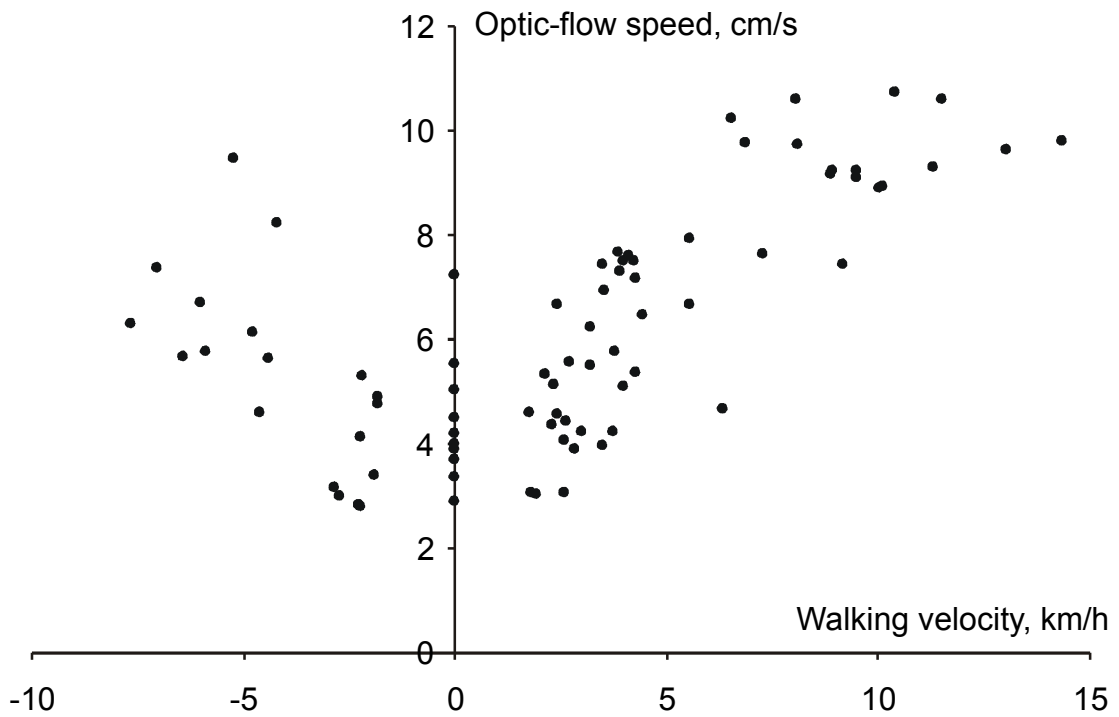


Figure 6 Influence of walking direction on the perceived speed of optic-flow for a single subject. Slopes are in the opposite direction to those presented previously due to reversal of the order of walking and standing (see chapter 5) such that an increase in matched optic-flow speed now represents a reduction in perceived optic-flow speed.

Subject	Forwards		Backwards	
	Slope	P	Slope	P
AP	0.35	0.0015	-0.39	0.1477
AT	0.19	1.69×10^{-09}	-0.11	0.0183
RH	0.52	2.74×10^{-16}	-0.39	0.0037

Table 2 Summary of influence of forwards and backward walking, showing the slope reversing with walking direction. Slopes are of opposite sign to those presented previously due to a change in the order of walking and standing (see Chapter 5).

Discussion

The findings of Thurrell et al. (1998) were confirmed with a population of naïve subjects, approximately 70% of whom (16 of 24) displayed a profound reduction of perceived optic-flow speed with increasing walking speed. Comparison of the intersubject mean effects revealed a steady reduction in effect strength as the activity became less similar to natural locomotion, with Finger Tapping alone having no significant influence on visual perception. Cycling utilises much of the same musculature as walking but with a different co-ordination pattern, and even for

experienced cyclists there would be no direct relationship between cadence and translational speed. Arm Pedalling utilises different muscles to those used in cycling, though with a broadly similar cyclical action. The most important similarity here is likely to be that between Arm Pedalling and the swinging of the arms that naturally accompanies walking. The reader can demonstrate for himself the importance of arm movements during walking by attempting to lock his arms to his body while walking, this is both awkward and feels unnatural. Another similarity could be between Arm Pedalling and our time as infants during which we crawl around on all fours, even though crawling infants are not renowned for their high rates of optic-flow! Finger Tapping utilises none of the same muscles as natural locomotion and it is hard to envisage it has any correlation with self-motion, and still less with providing locomotive force. This steady decline in effect strength, from locomotor-similar to locomotor-dissimilar movements, supports the hypothesis (Thurrell et al. 1998) that signals of limb movement are influencing visual motion perception via a mechanism, the normal purpose of which is to remove those optic-flow components that occur during, and as a consequence of, natural locomotion.

The hypothesis of Thurrell et al. (1998) would also predict that during backward walking this same mechanism would again act to remove those components of optic-flow resulting from translation of the eyes, resulting in an overestimation of optic-flow speed during faster backward walking. A more precise prediction would be that data points collected during backward walking would lie along an extension to the line of best fit through data points obtained during standing still and forward walking. The results, however, indicate that backward walking has the same effect as forward walking, i.e. faster backward walking also reduces the perceived speed of optic-flow, and this does not directly fit the hypothesis. Two modifications to the hypothesised mechanism can, however, explain all the results. 1) The simplest is that the direction of locomotion is ignored, perhaps as a consequence of the rarity of backward walking. 2) Backward walking is normally accompanied by contracting, not expanding, optic-flow. If the hypothesised mechanism was the result of learning, backward walking may influence only contracting optic-flow in the manner predicted. If at the same time, backward walking activated the mechanism due to its similarities to forward walking (much as the cycling action does), it would decrease the perceived optic-flow speed. This finding does, however, suggest that it is not the subject's intention or expectation of

the outcome of the action that alters perception, but rather the signals of limb movement, e.g. proprioceptive signals, themselves.

In conclusion, signals of locomotion from the limbs reduce the perceived speed of an optic-flow tunnel appearing to move towards the observer along the visual axis. The influence that such signals of locomotion exert on visual processing depends for its efficacy on the learnt or innate correlations between the motor activity performed, self-motion and the resulting optic-flow. The upper limbs, though not strictly locomotor in humans, may influence visual processing during Arm Pedalling due to similarities to the swinging of the arms that has been learnt to occur naturally during walking. Alternatively, if these visual-locomotor pathways have a genetic component, then as humans have quadrupedal ancestors, there may be vestigial quadrupedal pathways still active that may link both lower and upper limb movements to visual processing. The direction of the motor activity does not affect this mechanism, at least for walking, possibly due to a lack of experience, either of backward locomotion per se, or of the unusual combination of backward locomotion with expanding optic-flow. These results support the notion, proposed by Thurrell et al. (1998), that locomotor signals from the limbs are involved in visual processing as a means to reduce distortions of optic-flow components during translation through the environment.

Chapter 6

Reduction of perceived visual speed during walking: Selectivity for expanding optic flow components?

Abstract

During walking, it has been shown that efference copy, proprioceptive and somatosensory signals can be used as a measure of self-motion in order to distinguish self- and object motion (Thurrell et al. 1998). We investigated how these signals influence the visual processing of five progressively 'less' locomotor-like patterns of optic-flow and in three orientations relative to the direction of locomotion. The role of the primary visual cortex in this mechanism was also considered. Subjects viewed a target optic-flow pattern while walking at one of a variety of speeds in a virtual-reality simulator (Pelach et al. 1998). While standing still they were then required to manually adjust the speed of an otherwise identical optic-flow pattern to match the remembered speed of the target. The optic-flow patterns consisted of: an expanding tunnel of concentric rectangles; a horizontal grating translating downward; a vertical grating translating rightward; a cartwheel rotating about the axis of vision; and a flashing stationary tunnel (control). In agreement with previous findings, increased walking speed towards the visual scene resulted in a significantly lower perceived expanding tunnel speed in most subjects but had no significant effect on perceived flashing frequency. There were also smaller effects of walking on perceived grating speeds (horizontal greater than vertical) but not on perceived cartwheel rotation speed. In a complementary study, as the angle between visual direction and walking direction increased, the influence of walking speed on perceived tunnel speed decreased, whereas the influence on the perceived vertical grating speed increased. In a further study, a hemianopic 'blindsight' patient (GY) was tested to compare matching the tunnel speed between the intact and blind hemifields. No difference was found between the two hemifields: optic-flow speed perception in both was strongly influenced by walking speed. The results are explained in terms of a mechanism for maintaining visual perceptual constancy during locomotion.

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Introduction

As the retinae can only record the visual scene relative to themselves, during self-motion all visual motion signals will contain a component due to that self-motion and a component due to any object motion in space. Extraction of signals of object motion from visual input independent of self-motion is important in many tasks, for instance locating food, predators and for object recognition via perceptual grouping. During self-motion, for any given environment structure there is an equivalence between the optic-flow pattern observed and the properties (speed, direction and rotation) of the self-motion (Gibson, 1950, 1954, 1966). Gibson's motivation was that this equivalence could be used to extract a signal of eye motion in space that could be used for further visual processing such as computation of heading. However, the reverse is also true and if the properties of the self-motion are known from another source then they may be used to remove the distortions of the visual signal caused by the self-motion. A number of physiological sources may signal the position and velocity of the eyes in space, e.g. a combination of vestibular and extra-retinal signals (Wertheim 1994) or even global vision of the environment (Gibson, 1950, 1954, 1966). However, these sources each have their limitations e.g. the vestibular system has a poor response to self-motion during natural walking and visual determination of eye motion cannot occur when the environment is dark or lacking in depth cues (Warren and Hannon 1988).

During natural locomotion, i.e. overground walking, the vestibular system is unable to provide a reliable direct signal of motion due to its poor low frequency response, though it may provide a redundant measure of stride frequency, as this occurs within its optimal frequency range (Goldberg and Fernández, 1975). A more direct measure of walking speed could be obtained from an efference copy of central walking commands and proprioceptive and somatosensory signals from the legs themselves. Afferent signals from the legs have been shown to dominate over vestibular signals in self-motion perception under some circumstances (Hlavacka et al. 1996). It may be hypothesised that these signals, in combination with trunk and neck proprioception, would accurately signal eye motion relative to the support surface and hence (unless on a moving

walkway) the visual environment, and this would allow compensation for those optic-flow components introduced by walking. The perceived speed of expansion of an optic-flow pattern viewed head-on was shown to be influenced by walking speed in most subjects in a manner that could be explained by the perceptual constancy mechanism hypothesised above (Thurrell et al. 1998).

The proposed perceptual constancy mechanism suggests that the influence of walking speed would be specific to optic-flow patterns that are similar to those experienced during walking. This prediction may be quantitatively tested as it would result in a cosine-tuning between the directions of locomotion and apparent visual motion, i.e. the influence of walking speed would be proportional to the cosine of the angular difference between the walking and visual motion directions. We tested this prediction in the current study by including three other optic-flow patterns gradually becoming progressively less locomotor-like, and a non-moving (flashing) control pattern. Some changes in motion perception of visual stimuli have already been shown to be dependent on their global structure and proposed to be a consequence of their implied three dimensional motion (Bex and Makous, 1997). Often when walking we turn our heads to look at an object to the side or are otherwise not looking in the direction of travel. We would expect from the above mechanism that processing of visual scenes viewed to either side of the subject's direction of travel would reflect this change with a cosine tuning between the direction of walking and that of visual motion. Similar directional tuning has been found in studies of posture (Wolsley et al. 1996, Thurrell et al. 2000) where processing of the visual input or motor output was modified by the direction of gaze (head and/or eye rotation) relative to that of the feet. This was tested with the same optic-flow patterns as above with the relative alignment between walking and the visual axis being 0° (mid-line position), 45° (mid-right) or 90° (full-right).

At what stage of visual processing, and where in the brain the above mechanism of perceptual constancy may act, has not so far been investigated. Due to differences in locomotion between humans and other primates, single neurone recordings during walking are unlikely to be obtained and more indirect sources of information are required. Fortunately there is a large body of literature concerning the influence of eye movements on vision in primates to draw upon; though mostly concerned with eye-in-head motion some studies have investigated vestibular stimulation due to movements of the head. Most dorsal medial superior temporal (MSTd) neurones (in Rhesus monkeys)

have large receptive fields and are tuned to a continuum of first-order optic-flow motions (Graziano et al. 1994) making them ideal candidates for distinguishing self- and object-motion. Most MSTd neurones, unlike MT neurones, also respond selectively to externally induced visual motion and not to motion induced by eye movements (Erickson and Thier 1991, in Macaque monkeys) or head rotations (Shenoy et al. 1999, in Rhesus monkeys). Indeed, MSTd neurones have been shown to alter their receptive fields to compensate for the effects of eye movements (Bradley et al 1996, in a Rhesus monkey). Vestibular stimulation by linear whole-body movements also influences the directional selectivity of MST neurones in a manner that may disambiguate self- and object-motion (Duffy 1998, in Rhesus monkeys). This use of vestibular signals of self-motion in visual processing in MST and the notion that self-motion signals should interact with vision in the same way regardless of their source suggests MST as a likely candidate area to incorporate proprioceptively derived signals of self-motion.

After lesion of the primary visual cortex (V1), conscious vision is abolished, however, there may still be considerable residual visual function (though the subjects report that they do not 'see'), and this condition is referred to as 'blindsight' (see Barbur et al. 1980 and Stoerig and Cowey, 1997 for review). In patient GY, a lesion of the left primary visual cortex occurred during childhood rendering him hemianopic, but has since demonstrated residual visual function in the affected area (Barbur et al. 1980 and Morland et al. 1999). Part of GY's residual vision is the ability to make comparisons between the velocity of pairs of moving stimuli when either or both are presented in the blind hemifield (Morland et al. 1999). This residual velocity sensitivity must result from signals that bypass V1, such as those arising from the pulvinar via the superior colliculus that have been shown to be required for continued activity in MT after V1 lesions (Rodman et al. 1990). These signals may then continue to higher visual areas, such as MSTd where we predict they should interact with other signals, such as those of self-motion. GY was therefore used to test the prediction that walking speed should influence optic-flow speed perception in both the intact and blind hemifields.

Methods

Subjects stood or walked upon an exercise treadmill placed directly in front of a large rear projection screen (see Figure 1a and Pelah et al. 1998). The treadmill (Woodway Exo 43) was powered by the subjects themselves pushing against the handrails with their arms, an action similar to (though less arduous than) pushing a shopping trolley.

The walking speeds of the subjects were obtained from a sensor attached to the treadmill axis, which was electronically low pass filtered at 30Hz and then digitally sampled and low pass filtered at 30Hz and 7Hz respectively.

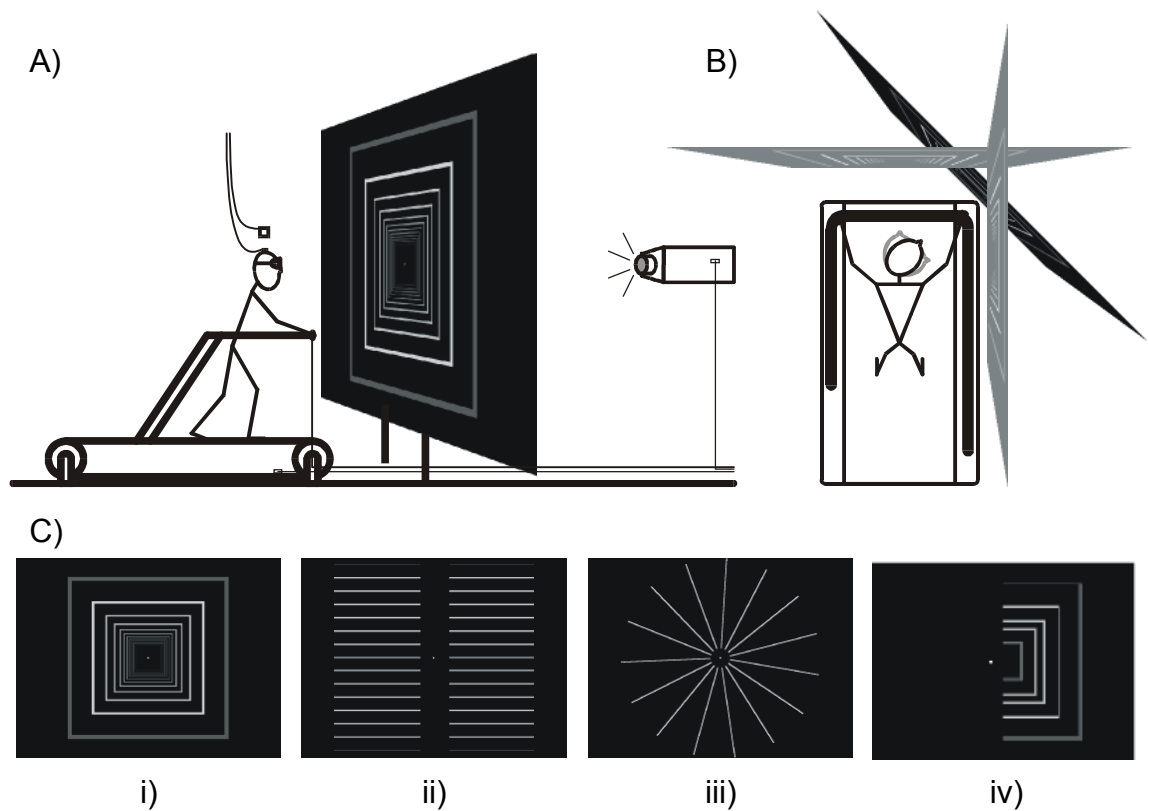


Figure 1 (a) The general set-up for the main study. (b) The alternative positions of the screen. (c) Screen shots of the various optic-flow patterns: i) the moving and flashing tunnels shared the same structure; ii) the horizontal and vertical gratings were identical but for orientation; iii) the rotating cartwheel and iv) the right half tunnel used to test the blind-sight patient showing the offset fixation point.

Optic-flow structure

The image projected on the screen was contained within a central area 1.9m wide by 1.52m high and approximately 0.9m from the subjects' eyes giving a viewing angle of 93° by 80° . Subjects wore welders goggles restricting peripheral vision and reducing the brightness by a factor of 100, thus ensuring that the border of the screen remained invisible at all times. The goggles also allowed only monocular vision, always with the right eye, removing stereoscopic depth cues. The visual scene was produced by an LCD projector (InFocus LP740) with a resolution of 1280 by 1024 pixels and a refresh rate of 60Hz updated on alternate frames. Five visual scenes were used for each

subject: (1) Moving Tunnel, (2) Horizontal Grating, (3) Vertical Grating, (4) Cartwheel and (5) a Flashing Tunnel. A fixation point 3 pixels square ($0.28^\circ \times 0.28^\circ$, luminosity 1.51 cdm^{-2}) was provided at the centre of the display approximately at each subject's eye level for all optic-flow patterns, the structure of the remainder of the scene being as follows.

(1, 5) The two tunnels were composed of a simulated square tunnel in depth (simulated relative dimensions, near-point relative to the observer = $0.4 \times$ width, far-point relative to the observer = $5 \times$ width) that consisted of 15 bright, anti-aliased squares against a dark background (0.006 cdm^{-2}), see Figure 1c. The squares obeyed laws of perspective: increasing in thickness and size with decreasing simulated distance from the observer and luminosity changing as a trapezoid function of simulated distance (maximum luminosity 1.51 cdm^{-2}). This allowed fading of the rectangles into the distance with perspective and a reduction in brightness near the border of the screen to remove edge flicker. (1) The Moving Tunnel simulated translation in depth with speed measured in the plane of the screen of tunnel components at the mid-hemifield position ($\sim 27.8^\circ$ away from fixation) thus at this point the 5 cm/s (expanding) target speed used corresponded to angular motion of 2.7° s^{-1} at each subject's eye. (5) The Flashing Tunnel exhibited sinusoidal variations in brightness of all tunnel components together with a target speed of 2.0 Hz .

(2, 3) The two gratings were composed of 15 bright, equally spaced, anti-aliased lines against a dark background. Lines extended across the full height (or a width equal to the height) of the screen except for a gap (10% of screen height) in the centre to prevent overlap with the fixation point. As lines neared the edges of the screen they faded into and out of existence with a trapezoid brightness profile (maximum luminosity 1.51 cdm^{-2}) to prevent edge flicker. Grating speed was measured as the distance traversed across the screen in centimetres, again the target speed being 5 cm/s . Other than orientation, horizontal and vertical gratings were identical, the Horizontal Grating always moving downward and the Vertical Grating always moving rightward.

(4) The Cartwheel was composed of 15 bright (luminosity 1.51 cdm^{-2}) spokes rotating anti-clockwise around the axis of vision, their overall diameter was equal to the screen height, with a blank gap with a diameter of 10% of the screen height around the fixation point. Cartwheel speed was measured in the same manner as the Moving Tunnel: that of

the components in the plane of the screen at the mid-hemifield position, the target speed was also 5cm/s.

Viewing Orientation

In a reduced number of subjects, the treadmill was rotated relative to the screen (see Figure 1b) by 0° (mid-line), 45° (mid-right) or 90° (full-right) and the experiment repeated using all five optic-flow patterns at each orientation. These subjects were instructed to view the scenes presented at the mid-right and full-right positions by rotating the head on the neck rather than the eyes in the head and to otherwise maintain the orientation of their bodies to that of the treadmill. The position and orientation of the head was monitored during the experiment using a Polhemus Fastrack magnetic position-sensing device providing six degrees of freedom. The receiver of this device was attached to a light helmet worn on the top of the head with position data being collected at 30 Hz.

For each optic-flow pattern, subjects were required to perform a matching task between the perceived velocity of a number of ‘target’ and ‘test’ scenes along the visual axis. These matches were made as a series of trials (see Figure 2): a 10s target presentation occurred during walking at one of six subjective speeds: ‘stationary’ (control), ‘very slow’, ‘slow’, ‘normal’, ‘fast’, or ‘very fast’ and was followed by two test presentations of 10s each during which no walking occurred. These trials are the same as type 1 trials in chapter 4. Instructions (‘target’ or ‘test’ and walking speed) were given visually with a fixation point during the 5s gap between each scene presentation. For the test scene presentations, the subjects used a rotating knob to control the velocity of the optic-flow pattern, this was attached to the right handrail of the treadmill such that subjects could rest their hands at all times while making an adjustment. At the beginning of each matching presentation this was reset to a negative optic flow velocity. The output of the knob was digitally sampled and low pass filtered at 30Hz and 7Hz respectively and then a small amount of noise was added to mask the pixel jitter at low tunnel speeds. A small random offset was also added to the knob position for each presentation to prevent subjects using knob position as a cue. Subjects were instructed before each experiment to be at the required walking speed before the scene became visible and to adjust the test scene as quickly and accurately as possible to match only the most recent target speed. For each visual pattern there were six matches at each walking speed, with five visual patterns giving a total session time of approximately 70 minutes. Subjects were rested

between optic-flow patterns and testing of different orientations for each subject occurred on separate days to reduce fatigue.

Data analysis occurred off-line with the mean walking speed and visual speed (or frequency) over the final 5s and 1s of scene presentation recorded respectively. Walking speeds were normalised as a proportion of the mean speed during the ‘very fast’ trials of that type and optic-flow speeds were normalised as a proportion of the target speed. A measure of setting accuracy was calculated as the standard deviation of the optic flow velocity and used to remove erroneous points by eye. Conditions were randomly ordered in all experiments. Subjects were given practice with treadmill walking at the various subjective speeds, and matching the visual scenes beforehand.

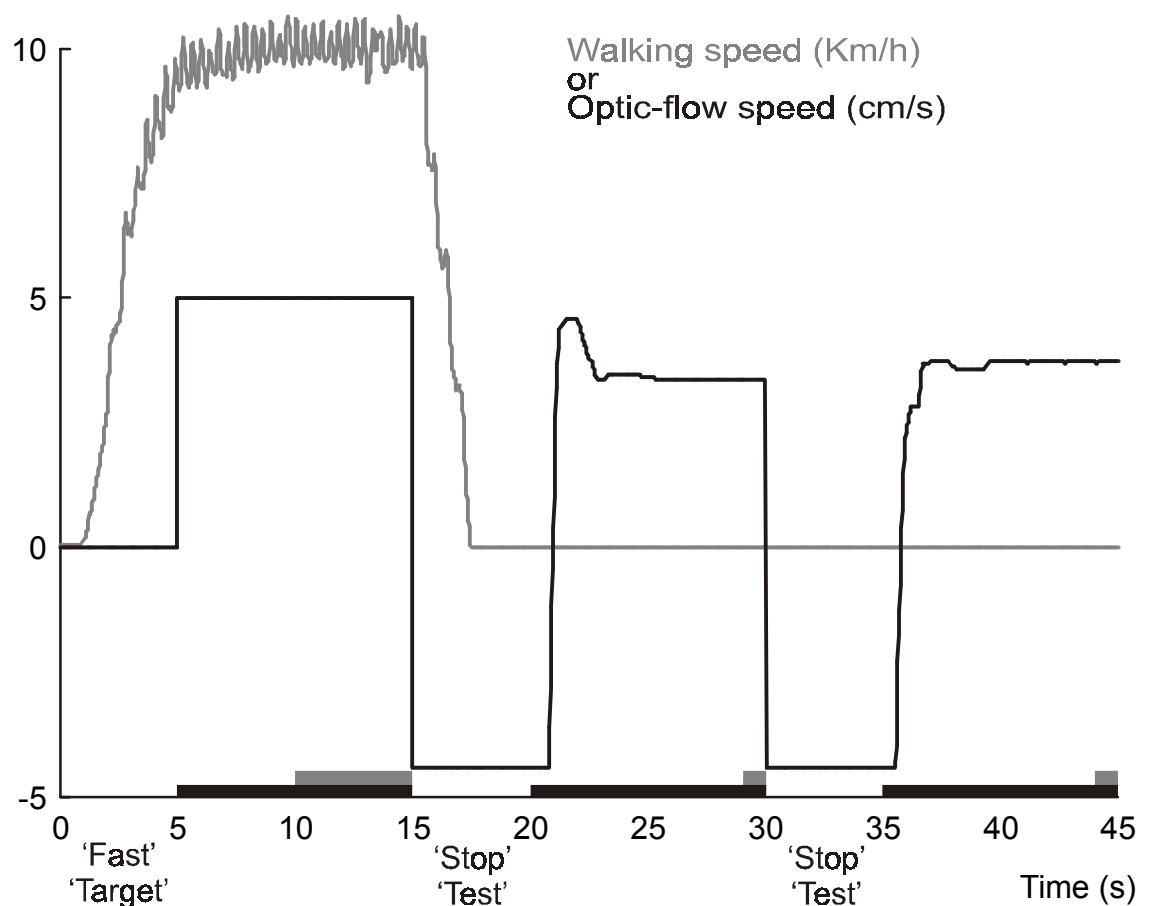


Figure 2 The time sequence of each trial. Instructions (printed below the time axis) were displayed for 5s each (thin portion of time-scale) alternating with the expanding tunnel (10s, thick portion). Mean settings during the last 1s (short grey bars) of each test tunnel were plotted against the mean activity speed during the last 5s (long grey bar) of the target tunnel.

Blindsight Patient

To enable independent testing of each hemifield of 'blindsight' patient GY, the Moving Tunnel was modified to enable presenting of only the left or right half at a time. The fixation point was also moved slightly away from the centre of expansion of the tunnel, as GY has some macular sparing in the blind hemifield and this ensured that the tunnel was only visible to the designated side (Figure 1c). GY has been shown to be able to accurately compare the velocities of stimuli when either are both are presented in the blind hemifield (Morland et al. 1999). In this modified experiment, the target optic-flow speed was displayed either to the blind hemifield or to the intact hemifield (control), but the test optic-flow presentation was always displayed to the intact hemifield. This allowed a conscious matching of the target speed irrespective of the side of target display.

Results

Main Effect

Walking speed had a profound effect on the values matched by subjects to the constant target velocity. An example of the influence of walking speed on the perceived speed of tunnel expansion is shown in Figure 3. 60% (9 of 15) of subjects tested showed a reduction of perceived tunnel optic-flow speed with increasing walking speed. The remaining six subjects either misinterpreted the instructions, reported becoming confused, or otherwise did not exhibit the reduction in perceived tunnel speed with increasing walking speed, and were therefore excluded from further analysis. The subject shown in Figure 3 shows a typical response from the group of interest: as the subject walks faster during the target presentation, the target tunnel is perceived to be moving slower, consequently during the test presentations the matched optic flow speed is lower. The strength of this effect can be measured by the slope of the line of best fit (normalised for target speed), which for this subject (AT) was -0.43 and significantly different from zero ($P < 10^{-8}$). The line of best fit intercepts the optical speed axis near the target speed indicating unbiased optic flow perception during standing.

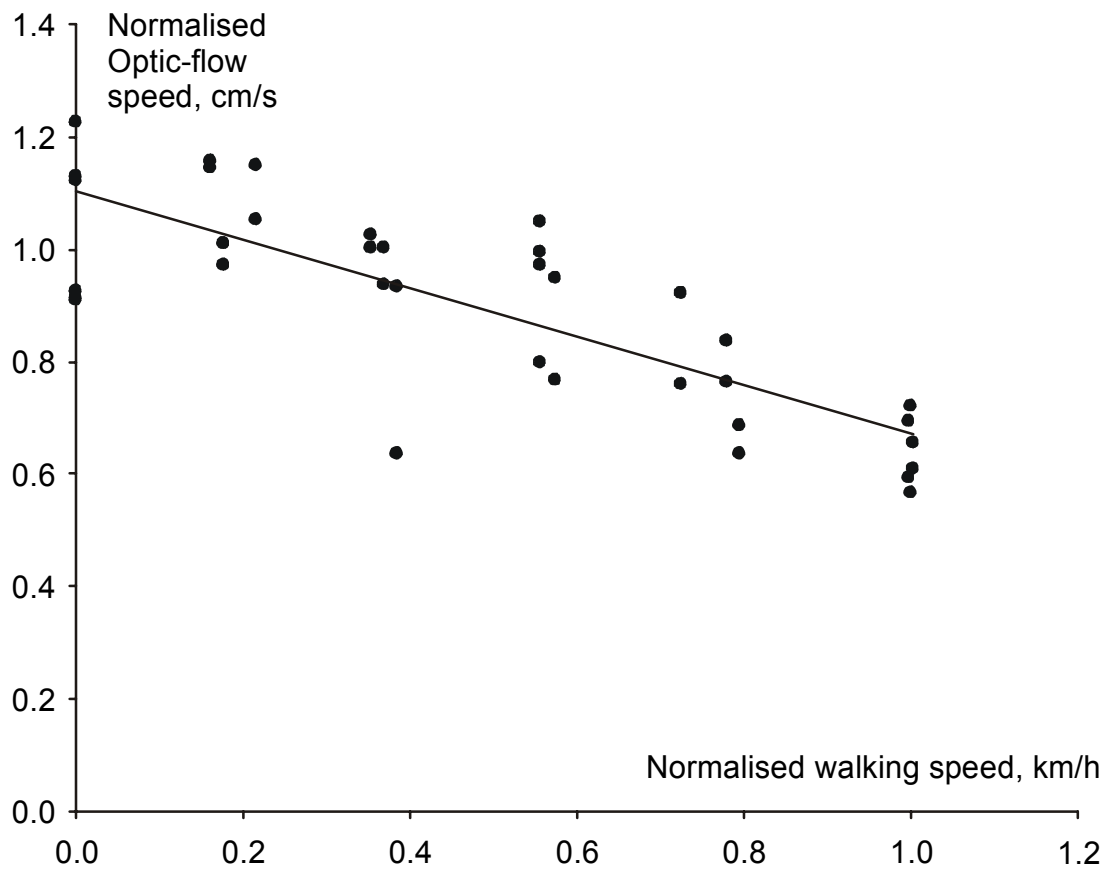


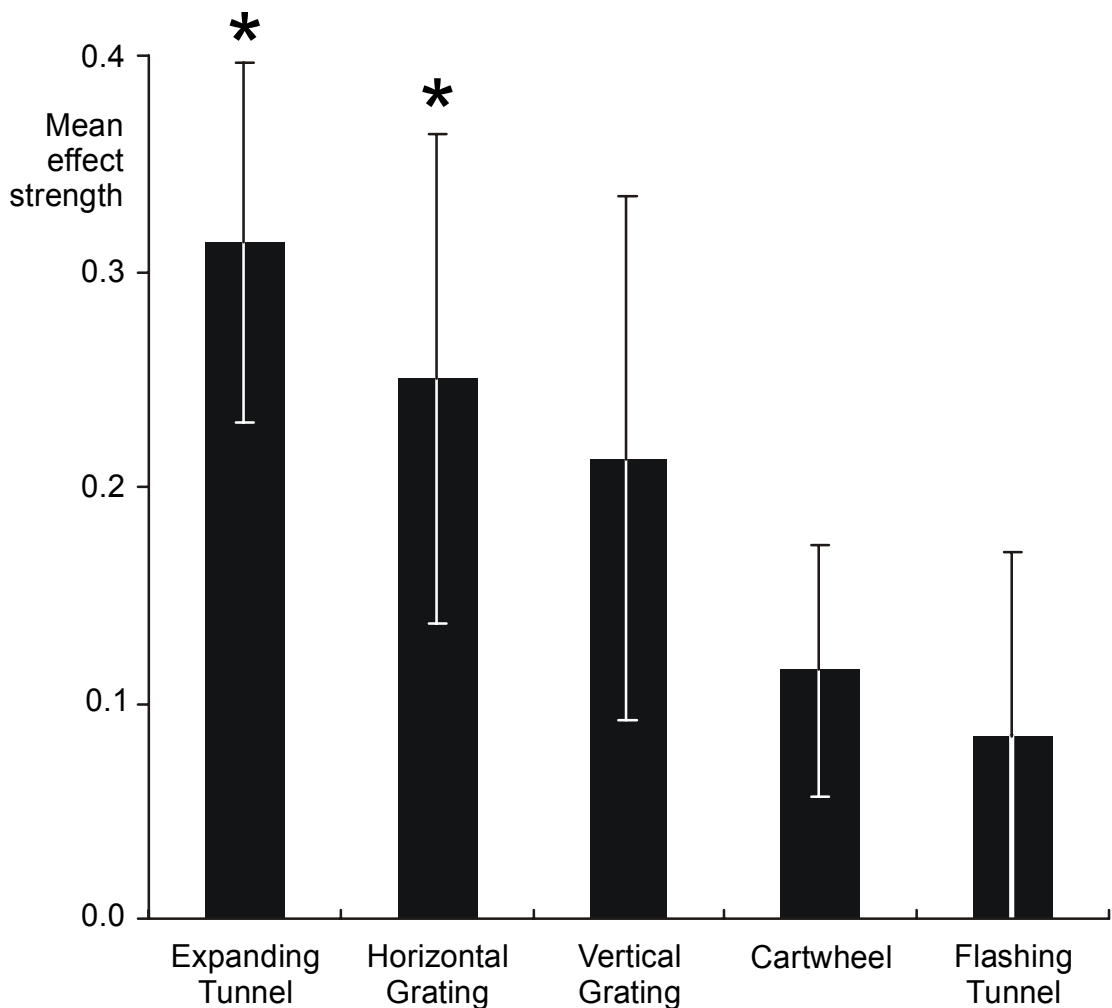
Figure 3 The basic effect of increasing walking speed reducing the perceived speed of expanding optic-flow. The similarity of the matched values to the target values when standing during both the target and the test can be seen (normalised data, target = 1). The line of best fit had a Y intercept of 1.10, a slope of 0.43 and was significantly different from

Subject	Moving Tunnel	Horizontal Grating	Vertical Grating	Cartwheel	Flashing Tunnel
AP	-0.36	-0.37	0.06	0.02	0.03
AT	-0.43	-0.28	-0.43	-0.07	-0.14
BW	-0.25	0.05	0.11	-0.06	-0.03
CJ	-0.07	0.02	0.01	-0.14	-0.06
JN	-0.24	-0.27	-0.23	0.02	0.00
MP	-0.09	0.10	-0.15	0.04	0.00
MO	-0.71	-0.66	-0.50	-0.53	0.13
MB	-0.66	-0.87	-0.96	-0.15	-0.74
RT	-0.01	0.02	0.17	-0.17	0.06
Mean	-0.31*	-0.25*	-0.21	-0.12	-0.08
S.E.M.	0.08	0.11	0.12	0.06	0.09

Table 1 Slopes of best-fit lines (i.e. effect strength) for all five optic-flow patterns for each subject. Comparison of means shows the trend from the moving to the flashing tunnel. * Denotes a significant difference from zero ($P < 0.05$).

Optic-Flow Structure

To determine the types of optic-flow pattern influenced by walking speed, subjects' visual motion perception was tested for each of the optic-flow patterns under otherwise identical conditions, and the results normalised both by maximum walking speed and visual target speed are shown in Table 1. The results show a trend in the strength of the influence of walking speed on optic-flow perception (see Figure 4) from the Moving Tunnel through the Horizontal Grating, Vertical Grating and Cartwheel to the Flashing Tunnel. Effect strengths for the Moving Tunnel and for the Horizontal Grating were significantly different from zero ($P < 0.05$), though not for the Vertical Grating, the Cartwheel or the Flashing Tunnel.



*Figure 4 Intersubject mean (\pm s.e.m.) strength of effect as measured by normalised slope showing the trend in effect magnitude from the Moving Tunnel to the Flashing Tunnel. Effect strengths for the Moving Tunnel and Horizontal Grating were significantly different from zero ($P < 0.05$), but not for the Vertical Grating, the Cartwheel or the Flashing Tunnel. * Denotes a significant difference from zero.*

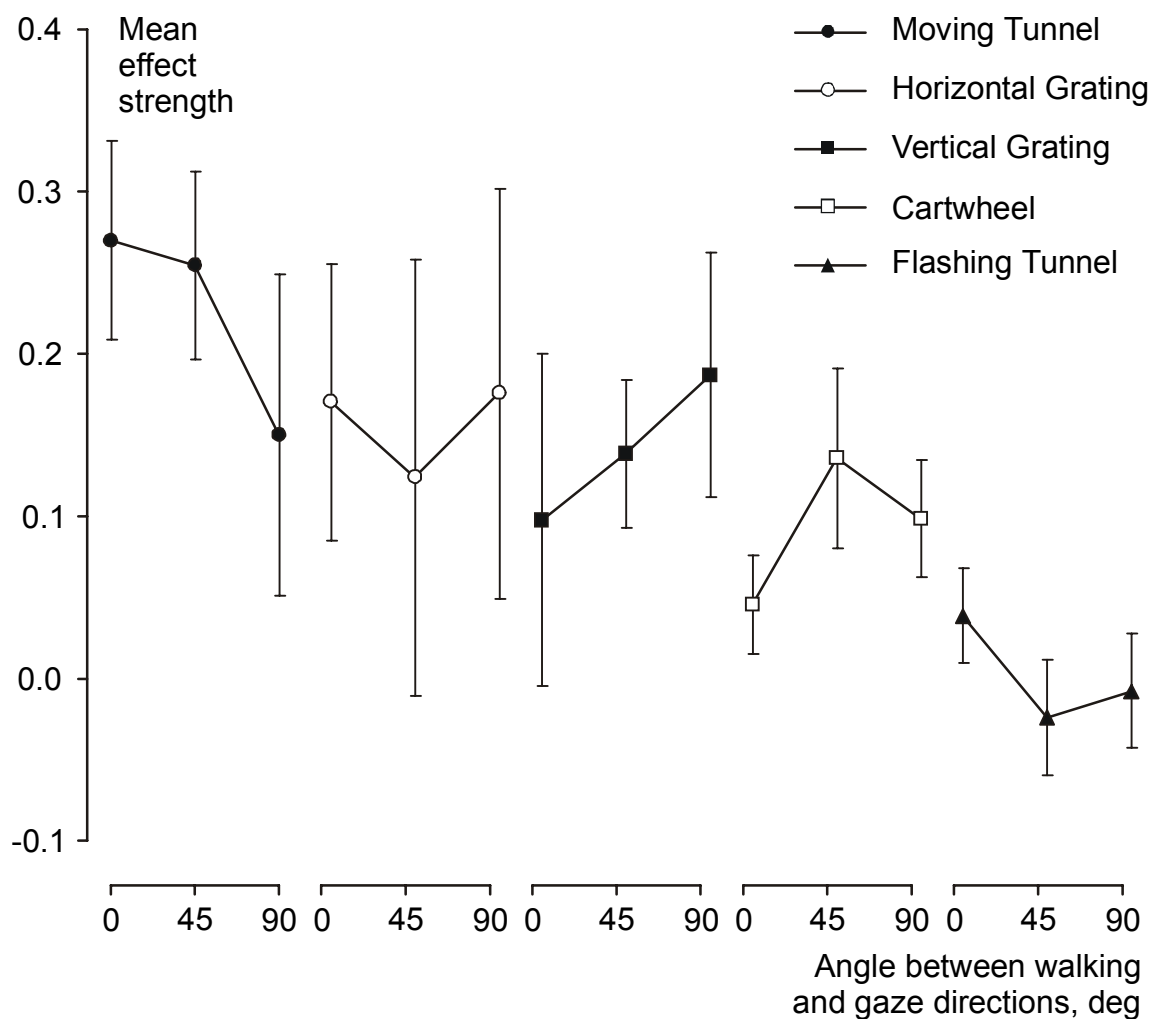


Figure 5 Influence of the orientation of walking direction on the perceived speed of optic flow. As the direction of walking and the direction of visual motion become more aligned (0° for the Moving Tunnel, 90° for the Vertical Grating) the influence of walking on the perceived speed of the optic-flow pattern becomes more pronounced. Walking speed has no effect on temporal perception of the Flashing Tunnel at any orientation. See main text for other conditions. Error bars denote s.e.m.

Viewing Orientation

Six subjects were used to investigate the tuning of the direction of walking relative to that of the axis of vision. One subject did not show a reduction of perceived tunnel optic-flow speed with increasing walking speed and was therefore excluded from subsequent analysis. The relative order of the strength with which walking speed affected the perceived speed of each optic-flow pattern at the 0° orientation was the same as for the complete group of nine subjects. However, as the angle between the walking direction and the visual axis increases, a number of trends are apparent: (1) The effect strength for the Moving Tunnel decreases by a factor of approximately two, with effect strength being significantly non-zero at both 0° (mid-line) and 45° orientation, but

not at 90° (full-right). The cosine tuning predicts that the influence of walking speed when viewing in the mid-right position would be 71% as great as its influence in the mid-line position, in practice this ratio was found to be 92%, i.e. not significantly different ($P > 0.05$). (2) The Horizontal Grating is not significantly different from zero at any orientation, though in the larger number of subjects tested in the mid-line position presented above, significance at the $P < 0.05$ level was achieved. For (3) the Vertical Grating and (4) the Cartwheel, effect strength increases by a factor of approximately two as the relative orientations increase and are significantly non-zero at 45° and 90°. The Vertical Grating also behaved consistently with the predictions of a cosine tuning between walking and visual motion directions, with effect strength in the mid-right position being 74% as great as during the full-right position (71% predicted). (5) The effect strength for the Flashing Tunnel is not significantly different from, and remains around, zero at all orientations. See Table 2 and Figure 5.

Scene	Orientation		
	0° (mid-line)	45° (mid-right)	90° (full-right)
Moving Tunnel	-0.27 ± 0.06*	-0.25 ± 0.06*	-0.15 ± 0.10
Horizontal Grating	-0.17 ± 0.09	-0.12 ± 0.13	-0.18 ± 0.13
Vertical Grating	-0.10 ± 0.10	-0.14 ± 0.05*	-0.19 ± 0.08*
Cartwheel	-0.05 ± 0.03	-0.14 ± 0.06*	-0.10 ± 0.04*
Flashing Tunnel	-0.04 ± 0.03	0.02 ± 0.04	0.01 ± 0.04

*Table 2 Summary of the influence of walking on perceived optic flow speed at different orientations and for different scenes. Effect strength is given as the mean (\pm s.e.m.) slope of line of best fit across five subjects. * Denotes a significant difference from zero.*

Blindsight Patient

Patient GY reported a sensation of movement when the Moving Tunnel was presented in his blind hemifield, though maintained that there was no conscious sensation of vision, in accordance with descriptions of residual vision. He showed a strong influence of walking on perceived Moving Tunnel speed when viewing both the target and test scenes with his intact visual hemifield giving an intercept of 5.19 and a slope of -0.89. GY was then tested twice viewing the target scene with his blind hemifield but viewing of the test scene with his intact hemifield, the lines of best fit having intercepts of 3.90 and 5.48 and slopes of -0.62 and -0.69 respectively (unnormalised data). The size of the slope is slightly higher during viewing with the intact hemifield, however, the large overlap of data points (see Figure 6) reveals no significant difference.

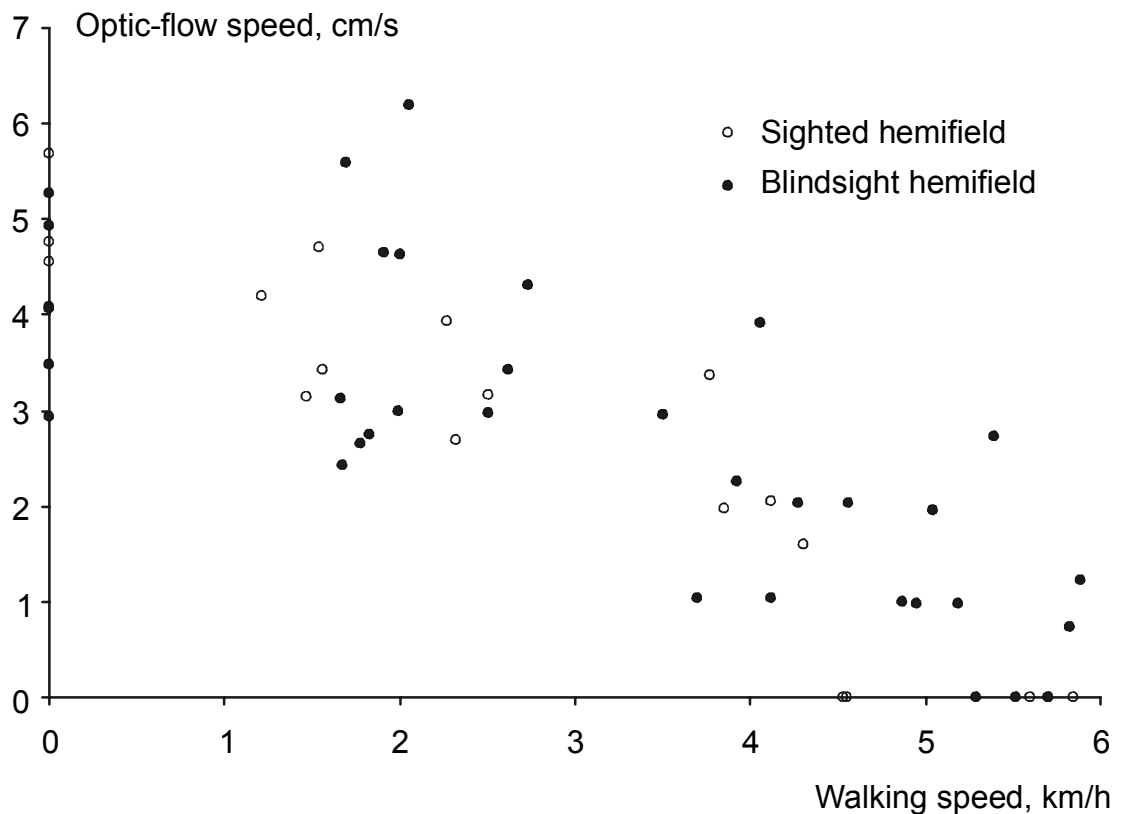


Figure 6 Comparison of changes in perceived optic-flow speed of the modified Moving Tunnel during walking between the normally sighted and blind-sighted visual hemifields of patient GY. The target tunnel was viewed with either the intact sighted hemifield (open circles) or the lesioned blind-sighted hemifield (solid circles), while matching was conducted using only the intact hemifield in both cases.

Discussion

In a population of naïve subjects, 60% (9 of 15) displayed a prominent reduction of perceived expanding optic-flow speed with increasing walking speed, confirming the findings of Thurrell et al. (1998). Comparison of the intersubject mean effects during mid-line viewing revealed a steady reduction in effect strength as the optic-flow pattern became less similar to that experienced during natural locomotion. This parallels the results of chapter 5 where the effect strength reduced as the motor activity became less correlated with forward motion, i.e. it is the match between the activity and the visual consequences that is important. (1) Expanding optic-flow was strongly influenced by walking speed such that for some subjects at the higher walking speeds the target actually appeared to be stationary. (2, 3) The two gratings contain no global expanding optic-flow components, and therefore no influence of walking speed might be expected.

However, non-linearities in the system may result in those regions of the gratings moving in the same direction as the expanding tunnel (the right or lower hemifields) overpowering those regions containing a contracting component. Both the (downwards drifting) Horizontal Grating and the (rightwards drifting) Vertical Grating showed smaller effects than the Expanding Tunnel, with the Horizontal Grating showing a significant effect marginally greater than that of the Vertical Grating, which did not reach significance. A possible explanation for a greater effect on the horizontal than on the vertical grating could be that when walking outside or in a building with a high ceiling, the optic-flow components present in the upper hemifield of vision are absent or very much reduced. Consequently, the downward motion of the grating corresponds well to the motion of the floor in the lower hemifield whilst containing less conflict with the 'expected' optic-flow components in the upper hemifield of vision. A more detailed study would be required to confirm or refute this difference. (4) The Cartwheel also contains no expanding optic-flow components overall, but neither does it contain local motion at any point that matches that in the Expanding Tunnel, as motion at all points occurs orthogonal to expanding motion. Therefore the Cartwheel was not expected to be influenced by walking speed when in the mid-line position and this was confirmed; perception of rotating optic-flow using the Cartwheel showed no significant influence of walking speed.

A possible alternative explanation for the influence of walking speed on visual motion perception would be that motion of the head resulting in vestibular stimulation causes an increase in visual motion detection thresholds and latencies (see Probst et al. 1986). This may extend to a reduction of perceived supra-threshold visual motion speeds during concomitant head motion. The lack of influence of walking speed on the perceived Cartwheel speed suggests that this mechanism is not at play here, in support of previous studies (chapter 5). (5) The Flashing Tunnel served as a control in that it contained absolutely no motion components, but involved matching temporal frequency, therefore no influence of walking speed was expected, confirming the results of Thurrell et al. (1998).

The mechanism proposed to help maintain perceptual constancy of vision predicted that as the direction of self-motion, as indicated by signals of walking, becomes more different from the direction of visual motion, then the influence of walking speed on visual perception would decrease. When the Expanding Tunnel (with apparent motion

along the line of sight) was viewed to the side during walking, there was a reduction in the influence of walking speed and this reduction was consistent with a cosine tuning of the proposed mechanism. The (rightward drifting) Vertical Grating also behaved consistently with the predictions of a cosine tuning between walking and visual motion directions. Effect strength for the (downward drifting) Horizontal Grating was not significantly different from zero at any orientation in those subjects tested looking to the side and showed no trend between orientations, motion always being orthogonal to the walking direction, which follows the cosine tuning prediction. However, in the mid-line position using all the subjects, there *was* a significant influence of walking speed on the Horizontal Grating perception, and this may have a different explanation (see above). The Cartwheel showed an increase of effect strength to achieve significance in both the mid-right and full-right orientations; this was somewhat unexpected, as the Cartwheel contains no overall direction of motion. However, an explanation may be provided by a theoretical analysis of the components of optic-flow patterns (Koenderink, 1990). The rotation component of an optic-flow pattern, e.g. the cartwheel may, at any instant in time, with equal validity be considered as a combination of vertical shear and horizontal shear. During outdoor walking the visual scene may often be approximated by a ground plane, as forward motion occurs those parts of the ground near to the subject appear to move backwards faster than those further away, in essence at any moment the ground appears to be undergoing a shearing motion. This may be easily demonstrated by the reader looking sideways out of the window whilst they are a passenger in a train or car moving through a flat landscape. As walking speed increases, with the visual axis off centre the above mechanism of perceptual constancy may reduce the shear component of the Cartwheel rotation, thus reducing the overall perceived speed of rotation. The Flashing Tunnel remained unaffected by walking speed at all orientations as expected from the proposed mechanism (Thurrell et al. 1998).

In GY's blind hemifield, those visual signals that would normally travel via area V1 are unavailable, GY's remaining abilities in this hemifield, i.e. his residual vision, must therefore depend on alternative pathways. The residual vision demonstrated here, the ability to sense and compare the velocity of moving stimuli, is thought to occur in area MT, using visual signals from the superior colliculus via the inferior pulvinar nucleus (see Rodman et al. 1990). GY's ability to make repeatable velocity comparisons between the blind and intact hemifields is consistent with use of these remaining pathways. Regarding the influence of locomotion speed on visual motion perception, as

this also occurs in GY's blind hemifield, and also with a strength comparable to that in the intact hemifield, V1 must not be required for this mechanism. MSTd is directly above area MT in the visual processing hierarchy and has a number of demonstrable properties that would make it suitable for combining walking and optic-flow signals: many MSTd neurones, unlike MT neurones, respond selectively to externally induced visual motion but not to motion induced by eye movements (Erickson and Thier, 1991) or head rotations (Shenoy et al. 1999). Vestibular stimulation by linear whole-body movements also influences the direction selectivity of MST neurones in a manner that may disambiguate self- and object-motion (Duffy 1998, Bremmer et al. 1999). Signals of eye motion (whether this is eye-in-head motion or locomotion of the whole body) must interact with retinal signals to compensate for those eye movements either early or late (van den Berg and Beintema 1997). In the former, compensation for eye movements occurs before local velocity signals are combined into signals of global flow, whereas in the latter, signals of global flow are created first and these are then altered to result in compensated global signals of optic-flow. In the first possibility, the same compensation must occur (in the intact hemifield) in two pathways: in the geniculo-striate pathway and in the tecto-fugal pathway. In the second possibility, the compensation need only occur in one place (probably in MSTd), and this must be considered the more likely scenario.

In conclusion, signals of walking speed are proposed to be combined with visual signals, at a level no lower than area MT though probably in MSTd. This occurs as part of a mechanism whose function is to reduce the distortions of visual motion that occur as a consequence of translation of the eyes through the environment. This mechanism is tuned to those optic-flow components expected as a result of both locomotion speed and orientation of the eyes relative to the direction of travel and taking into account possible environmental structures with respect to experience.

Summary and Conclusions

In this thesis a number of interactions between signals of self-motion are investigated. Each of these signals is only one of the possible signals of self-motion used by the human brain and therefore would normally act in concert with the other signals as shown in chapter 4. The first two chapters described experiments using postural sway as a measure of the combined self-motion signal after manipulation of its visual or proprioceptive components. The next three chapters described investigations on how efference copy and proprioceptive signals influence visual motion processing, presumably by acting as signals of self-motion.

Visual signals of self-motion arise in retino-centric co-ordinates, whereas postural control presumably acts in body-centric co-ordinates, such that during the visual control of posture, unless the two are aligned physically, an internal reorientation must occur. In Chapter 2, the reorientation of visual signals of self-motion during rotations of the head and eyes in relation to the trunk was investigated. Previous experiments (Wolsley et al. 1996) had shown an accurate reorientation of this self-motion signal during head and/or eye rotations in a visible, well-structured environment. However, whether this reorientation could still occur without the cognitive cues afforded by a visible background, i.e. whether proprioceptive and efference copy signals of neck position were sufficient for this reorientation was unknown. This was tested using visually evoked postural sway as a tool to determine the direction of the resultant signal of self-motion for various directions of the visual motion signal. Cognitive cues were reduced or removed by performing the experiment in the dark and using an unexpected sequence of visual motion directions. The results showed that the visually evoked postural response and, therefore, the self-motion signal, were always aligned with the physical direction of the visual motion, regardless of the position of the eyes with respect to the trunk. Therefore, the hypothesis that proprioceptive and efference copy (signals of muscle commands, i.e. of the intended motion) signals of neck position are sufficient to reorient visual signals of self-motion used in the control of posture is supported.

Though proprioceptive and efference copy signals are sufficient to effect this reorientation of visual self-motion signals, conscious, cognitive influences may still have their part to play. In chapter 3, the accuracy of this reorientation was compared during conscious sensation of self-motion (vection) and conscious sensation of self-

stationarity (object-motion perception). The accuracy and magnitude of the direction of sway, and hence of the self-motion signal, were greater duringvection than object-motion perception, suggesting that conscious perception of self-motion may improve processing of the visual signal. As conscious perception is thought to arise at cortical levels, these findings suggest that the cortex is one of the places where retinal motion signals are reoriented by gaze direction.

Together the results presented in chapters 2 and 3 suggest that cognitive processes, though helpful, are not required for reorientation of retinal motion signals and as such form an important modulating influence on other pathways in the network presented in chapter 4. The improvements found with conscious self-motion perception would also seem to support the hypothesis that the postural response to large-field visual motion is a 'corrective' response to the 'detected' self-motion.

As vision is a predominantly exteroceptive sense, self-motion, or more accurately motion of the retinae, alters the retinal signal from what it would be without concurrent retinal motion. This alteration to the retinal signal may be used in the Gibsonian sense (1950, 1954, 1966) to reconstruct a signal of eye-, and consequently self-, motion, such as that used in the visual control of posture (see chapters 2 and 3). However, for tasks requiring a signal of an object's position or motion in space this alteration to the retinal signal must be removed. The structure of the environment and the motion of the eyes through this environment exactly determine the properties of this alteration. A number of non-visual signals may be used to determine eye- and self-motion, as presented in chapter 4, and in conjunction with knowledge of environmental structure, itself gained from vision, may be used to discount the visual alterations resulting from self- and eye-motion. In the second half of the thesis, three studies were presented investigating the use of efference copy and proprioceptive signals of self-motion from the legs to remove these visual alterations.

In Chapter 4, a comparison was made between visual motion perception when standing still and when walking on an exercise treadmill. Under these (walking) conditions, efference copy and proprioceptive signals of locomotion were dissociated from their visual consequences. By observing changes in motion perception of a constant visual stimulus during walking, the properties of the normal compensatory mechanisms may be inferred. The hypothesised compensatory mechanism involves discounting those components of visual motion that would normally be due to self-motion (walking) in

order to reveal motion of visual objects in space. These compensatory mechanisms were shown to behave as would be expected from the use of locomotor signals in the determination of eye-motion and therefore would be compatible with an extension to the concept of a reference signal of eye movement (Wertheim, 1994). In chapter 5 this influence of signals of walking was compared to signals from other motor activities less strongly linked to self-motion, e.g. finger tapping should not indicate self-motion at all. There was shown to be a tuning of the mechanism responsible for motor activities indicating self-motion i.e. in the conditions tested, for the similarity between the motor activity and walking. This agrees with predictions that the effect would be weaker for those activities that are less correlated with and consequently would be less reliable as indicators of self-motion. Likewise, using combinations of different patterns of optic-flow and walking directions, it was shown in chapter 6 that as the visual motion becomes less consistent, either in structure or direction, with the self-motion indicated by the current efference copy and proprioceptive signals, the influence of these signals on visual perception decreases.

In conclusion, there is a network of signals of self-motion, each with advantages and disadvantages that are combined dynamically so as to produce a single model of motion of the body and its parts. This model may be used to control that self-motion as in chapters 2 and 3 or to compensate for the effects of that motion on other sensory processes as in chapters 4 - 6 and as such must be considered when investigating any of its individual components.

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Appendix 1

The effect of stereoscopically and parallax defined scale on the strength of the arthrovisual effect

Introduction

During self-motion, for any given environment structure there is an equivalence between the optic-flow pattern observed and the properties (speed, direction and rotation) of the self-motion (Gibson, 1950, 1954, 1966). Gibson suggested that this equivalence could be used to extract a signal of eye motion in space that could be used for further visual processing. However, the reverse is also true and if the properties of the self-motion are known then they may be used to remove its influence on the visual signal. The reduction in perceived optic-flow speed during locomotion (chapters 4, 5 and 6) was shown to be consistent with such a mechanism to maintain perceptual constancy during self-motion. If this mechanism does act to maintain perceptual constancy during walking then it will reduce the perceived optic-flow speed by an amount equal to the walking speed. However, previously the optic-flow stimulus has been lacking a spatial scale preventing this prediction from being quantitatively tested: in the absence of any scaling information, any moving visual object may be small, close and moving slowly or it may be larger, further away and moving more quickly. A spatial scale may be provided using inherently scaled objects (i.e. those of a learnt constant size) or using stereoscopic, parallax, or accommodative signals. Stereopsis and parallax are able to accurately specify spatial scale over the range required for this experiment and rely on fewer assumptions (knowledge of inter-ocular distance) by the visual system, compared to using the interpretation of objects with an inherent scale. They may also be provided either together or independently, allowing spatial scale to be strongly or weakly defined respectively. The prediction that the arthrovisual effect reduces perceived visual motion by an amount that compensates for the walking speed was tested by providing a spatial scale using stereopsis and/or parallax signals in the visual stimulus.

Methods

Subjects stood or walked upon an exercise treadmill placed directly in front of a CRT monitor (see Figure 1). The treadmill (Woodway Exo 43) was powered by the subjects

themselves pushing against the handrails with their arms, an action similar to pushing a trolley. The walking speeds of the subjects were obtained from a sensor attached to the treadmill axis, which was electronically low pass filtered and digitally sampled at 30Hz. The positions of the eyes in space were monitored during the experiment using a Polhemus Fastrack magnetic position-sensing device. The receiver of this device was attached to a light helmet worn on the top of the head with eye positions calculated as rigid displacements from this position. Position data for each eye was collected at 30 Hz.

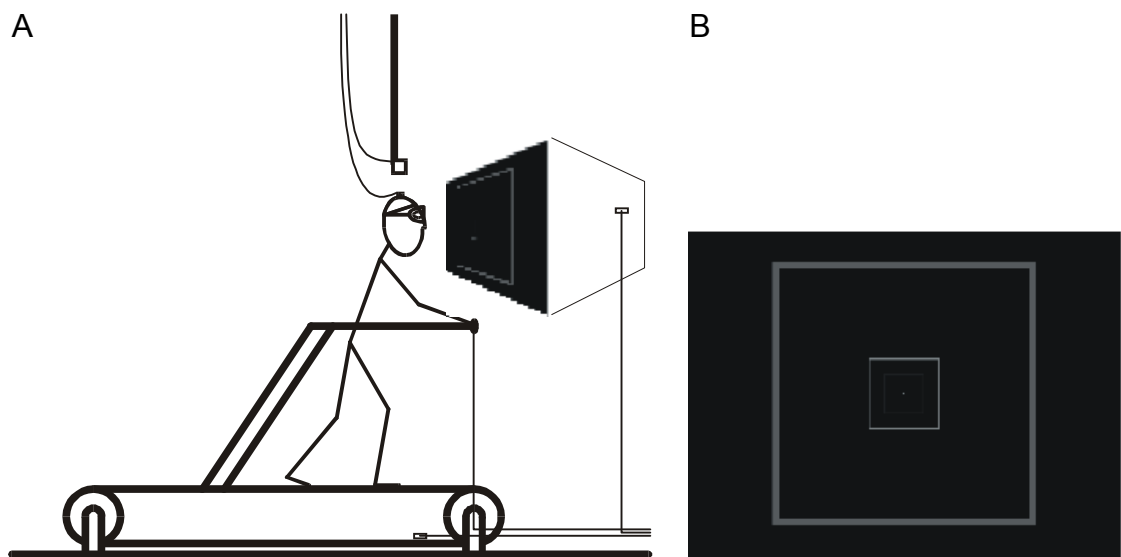


Figure 1 a) The experimental set-up, subjects wore stereoscopic occluding goggles and the head tracking receiver at all times. b) Reconstructed screen-shot of the tunnel.

The CRT display was 32cm wide by 24cm high and during experimental trials it was approximately 25cm from the subjects' eyes giving a field of view of $\sim 65^\circ$ by 51° . Subjects wore stereoscopic shutter goggles, restricting peripheral vision, though the entirety of the screen remained visible at all times, and with transmission ratios of $\sim 50\%$ (open) and $\sim 0.05\%$ (closed). The goggles allowed vision with only one eye at a time, synchronised with the CRT display to present alternate frames to the left and right eyes. The display had a resolution of 1280 by 1024 pixels, fully anti-aliased, and a refresh rate of 60Hz allowing presentation to each eye at 30Hz. The visual scene comprised a tunnel in depth composed of two or three bright squares on a dark background. The tunnel had simulated dimensions of width 2m, height 2m, near point 2m behind the display screen, length 6m and component line width of 10cm. Perspective projection with these parameters gave the tunnel an approximately similar appearance to that

during previous experiments (chapters 2, 3 and 4) except for the reduced number of tunnel components. A fixation point 1.2cm in diameter was simulated, floating in space 6m behind the display screen and at the same height above the floor of the tunnel as the subject's eyes. The luminosity of the tunnel components again changed as a trapezoid function of simulated distance. This allowed fading of the rectangles into the distance with perspective and a reduction in brightness near the limits of the display to remove edge flicker and prevent apparent vignetting of the tunnel by the display edges. The tunnel simulated translation in depth with the target speed used being equal to 3.1 kmph, this gave a mid-hemifield angular speed at the subjects' eyes of 4.0°s^{-1} , marginally faster than in the main experiments in chapters 4, 5 and 6.

Subjects were required to perform a matching task between the perceived velocity of a number of 'target' and 'test' tunnels along the visual axis. These matches were made as a series of trials: a 10s target presentation occurred during walking at one of six instructed speeds: 'stationary' (control), 'very slow', 'slow', 'normal', 'fast', or 'very fast' and was followed by two test presentations of 10s each during which no walking occurred. This order corresponds to those of the type 1 trials in chapter 4. Instructions ('target' or 'test' and walking speed) were given visually with a fixation point during the 5s gap between each tunnel presentation. For the test presentations, the subjects used a rotating knob to control the velocity of the tunnel, this was attached to the right handrail of the treadmill such that subjects could rest their hands at all times while making an adjustment. At the beginning of each matching presentation this was reset to a negative (contracting) tunnel velocity and a small random offset was also added for each presentation to prevent subjects using the initial position as a cue. The output of the knob was digitally sampled at 30Hz. Subjects were instructed before each experiment to be at the required walking speed before the tunnel became visible and to adjust the test tunnel as quickly and accurately as possible to match only the most recently presented target speed.

Tunnel stimuli could be presented with and without stereoscopic depth and with and without motion parallax information, therefore, there were four types of tunnel: (1) Control, with both parallax information and stereopsis indicating a flat scene at the distance of the display screen. (2) With only stereopsis indicating a three dimensional tunnel. (3) With only motion parallax indicating a three dimensional tunnel. (4) Full 3D with both motion parallax and stereoscopic depth. Subjects were each tested using three out of the four types of tunnel corresponding to absent (1), weak (2 or 3) or strong (4)

specifications of tunnel scale. For each tunnel there were 6 matches at each walking speed, with five visual patterns giving a total session time of approximately 45 minutes, subjects were rested between tests to reduce fatigue, which was higher during these than during previous experiments.

Data analysis occurred off-line with the mean walking speed and visual speed over the final 5s and 1s of target and test tunnel presentation calculated respectively. A measure of setting accuracy was calculated as the standard deviation of the optic flow velocity and used to remove erroneous points by eye. Conditions were randomly ordered in all experiments. Subjects were given practice with treadmill walking at the various instructed speeds and matching the tunnel speeds, their stereopsis was also tested beforehand.

Results

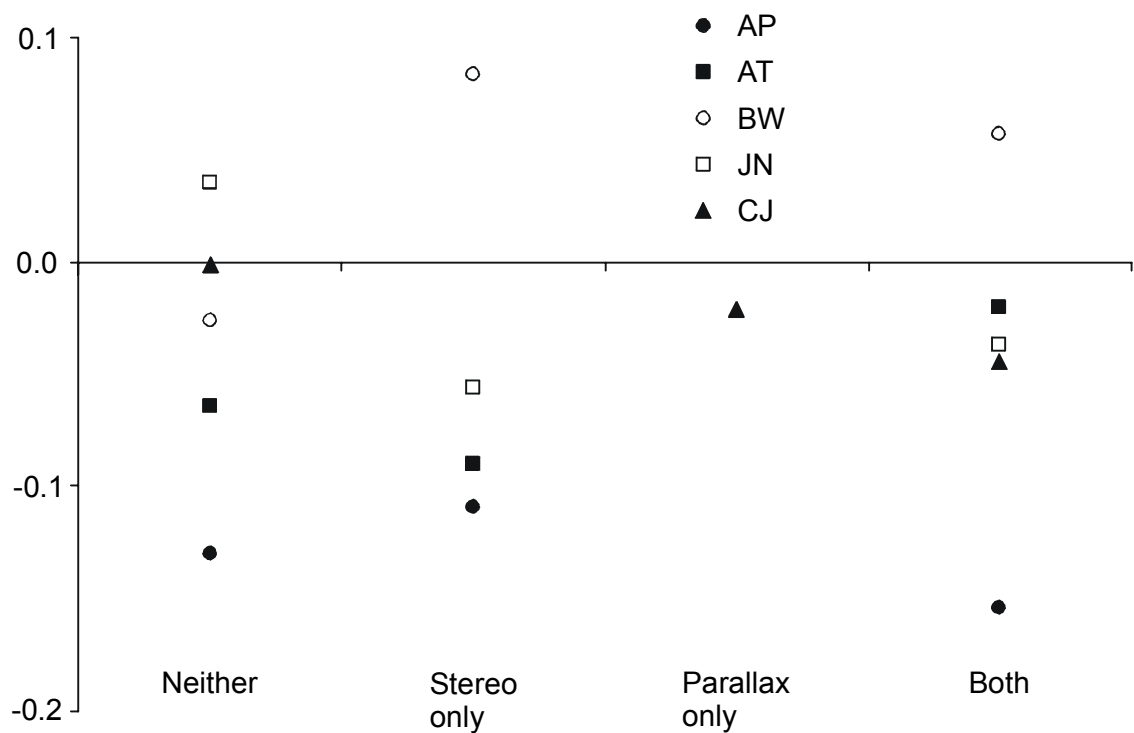


Figure 2 Effect strengths as measured by the slope of the line of best fit between perceived tunnel speed plotted against walking speed for each subject. All subjects were tested in the control and full 3D conditions, with subjects AP, AT, BW and JN also tested in the stereo only condition and subject CJ tested with parallax only.

All five subjects tested were known to have a strong, reliable reduction in perceived tunnel expansion speed during walking (see chapter 6). However, whilst one subject (AP) maintained a strong influence of walking speed on perceived tunnel speed across

the new conditions, for the remainder there seemed to be no consistent effect and a large variability between conditions (see Figure 2).

Discussion

Contrary to their previous performances (see chapter 6) four of the five subjects showed no significant reduction in perceived tunnel speed during walking in any condition, and for the remaining subject the effect was weaker than during previous experiments (see chapters 4, 5 and 6). Subject CJ displayed a lack of stereoscopic vision, and though he commented that he did not perceive the tunnel as three-dimensional, his results were comparable to those of the other subjects. Certainly none of the subjects displayed an effect resulting in a slope of -1 between the perceived tunnel speed and walking speed, i.e. true perceptual constancy, as was predicted. This disappearance of the effect does not seem to be due to the presence or absence of either stereopsis or parallax as there is no apparent difference between the conditions. Possible reasons for the lack of an effect could be the strain on the subjects of maintaining a three-dimensional percept of the stimulus in the virtual reality environment. Factors such as accommodative mismatch from the close screen distance, time lag between subject motion and screen updating, and the simplified nature of the stimulus itself (two or three squares instead of 12 or 13). With technical refinements, most of these problems may be overcome and the prediction of a reduction in perceived tunnel speed equal to the walking speed may be tested. However, the last possibility, that the altered 'tunnel' structure, consisting of only two or three concentric squares at any one time, should be investigated further. With the reduced number of tunnel components, signals of the displacement of individual components become stronger relative to signals of velocity. If walking does not influence these displacement signals speed as are signals of motion then the lack of an effect here could be explained. With a more advanced three-dimensional stimulus and/or alternative stimuli that produce strong displacement signals, it should be possible to test these two possibilities.