

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.

Reference List

- Barbur JL, Ruddock KH, Waterfield VA (1980) Human visual responses in the absence of the geniculo-calcarine projection. *Brain* 103: 905-928
- Bex PJ, Makous W (1997) Radial motion looks faster. *Vision Research* 37: 3399-3405
- Biguer B, Donaldson IML, Hein A, Jeannerod M (1988) Neck muscle vibration modifies the representation of visual motion and direction in man. *Brain* 111: 1405-1424
- Bles W, Jelmorini M, Bekkering H, de Graaf B (1995) Arthrokinetic information affects linear self-motion perception. *Journal of Vestibular Research* 5: 109-116
- Blouin J, Okada T, Wolsley CJ, Bronstein AM (1998) Encoding target-trunk relative position: cervical versus vestibular contribution. *Experimental Brain Research* 122: 101-107
- Bradley DC, Maxwell M, Andersen RA, Banks MS, Shenoy KV (1996) Mechanisms of heading perception in primate visual cortex. *Science* 273: 1544-1547
- Brandt T, Buchele W, Arnold F (1977) Arthrokinetic nystagmus and ego-motion sensation. *Experimental Brain Research* 30: 331-338
- Bremmer F, Ilg UJ, Thiele A, Distler C, Hoffmann KP (1997) Eye position effects in monkey cortex. I. Visual and pursuit-related activity in extrastriate areas MT and MST. *Journal of Neurophysiology*. 77: 944-961
- Bremmer F, Kubischik M, Pekel M, Lappe M, Hoffmann K-P (1999) Linear vestibular self-motion signals in monkey medial superior temporal area. *Annals of the New York Academy of Science* 871: 272-281
- Brenner E (1991) Judging Object Motion During Smooth Pursuit Eye-Movements: the Role of Optic Flow. *Vision Research* 31: 1893-1902
- Brenner E, van den Berg AV (1994) Judging Object Velocity During Smooth-Pursuit Eye-Movements. *Experimental Brain Research* 99: 316-324

- Bridgeman B, Stark L (1991) Ocular Proprioception and Efference Copy in Registering Visual Direction. *Vision Research* 31: 1903-1913
- Britton TC, Day BL, Brown P, Rothwell JC, Thompson PD, Marsden CD (1993) Postural Electromyographic Responses in the Arm and Leg Following Galvanic Vestibular Stimulation in Man. *Experimental Brain Research* 94: 143-151
- Bronstein AM (1986) Suppression Of Visually Evoked Postural Responses. *Experimental Brain Research* 63: 655-658
- Buizza A, Léger A, Droulez J, Berthoz A, Schmid R (1980) Influence of otolithic stimulation by horizontal linear acceleration on optokinetic nystagmus and visual motion perception. *Experimental Brain Research* 39: 165-176
- Chaudhuri A (1990) Modulation of the motion aftereffect by selective attention. *Nature* 344: 60-62
- Clément G, Jacquin T, Berthoz A (1983) Habituation of postural readjustments induced by motion of visual scenes. In: Igarashi, Black (eds) Vestibular and visual control on posture and locomotor equilibrium. Karger, Basel, pp 99-104
- Crowell JA, Banks MS, Shenoy KV, Adersen RA (1998) Visual self-motion perception during head turns. *Nature Neuroscience* 1: 732-737
- Daunton N, Thomsen D (1979) Visual modulation of otolith-dependent units in cat vestibular nuclei. *Experimental Brain Research* 37: 173-176
- de Graaf B, Bos JE, Wich S, Bles W (1994) Arthrokinetic and Vestibular Information Enhance Smooth Ocular Tracking During Linear (Self-)Motion. *Experimental Brain Research* 101: 147-152
- Dichgans JM, Held R, Young LR, Brandt T (1972) Moving visual scenes influence the apparent direction of gravity. *Science* 178: 1217-1219
- Dichgans JM, Brandt T, Held R (1975) The role of vision in gravitational orientation. *Fortschritte der Zoologie* 23: 255-263
- Duffy CJ (1998) MST neurons respond to optic flow and translational movement. *Journal of Neurophysiology* 80: 1816-1827

- Eklund G (1969) Influence of muscle vibration on balance in man. A preliminary report. *Acta Societatis Medicorum Upsaliensis*. 74: 113-117
- Erickson RG, Thier P (1991) A neuronal correlate of spatial stability during periods of self-induced visual motion. *Experimental Brain Research* 86: 608-616
- Fushiki H, Sato Y, Miura A, Kawasaki T (1994) Climbing fiber responses of Purkinje cells to retinal image movement in cat cerebellar flocculus. *Journal of Neurophysiology*. 71: 1336-1350
- Gdowski GT, McCrea RA (2000) Neck proprioceptive inputs to primate vestibular nucleus neurons. *Experimental Brain Research* 135: 511-526
- Gibson JJ (1950) The problem of the stable and boundless visual world. The perception of the visual world. Houghton Mifflin, Boston, pp 145-162
- Gibson JJ (1954) The visual perception of objective motion and subjective movement. *Psychological Review* 61: 304-314
- Gibson JJ (1966) The pickup of ambient information: scanning. The senses considered as perceptual systems. Houghton Mifflin, Boston, pp 250-265
- Gielen CCAM, van Asten WNJC (1990) Postural Responses To Simulated Moving Environments Are Not Invariant For The Direction Of Gaze. *Experimental Brain Research* 79: 167-174
- Goldberg JM, Fernandez C (1975) Vestibular mechanisms. *Annual Reviews in Physiology* 37: 129-162
- Goodwin GM, McCloskey DI, Matthews PB (1972) Proprioceptive illusions induced by muscle vibration: contribution by muscle spindles to perception? *Science* 175: 1382-1384
- Graziano MSA, Andersen RA, Snowden R (1994) Tuning of MST neurons to spiral motions. *Journal of Neuroscience* 14: 54-67
- Gregoric M, Takeya T, Baron JB, Bessineton JC (1978) Influence of vibration of neck muscles on balance control in man. *Agressologie* 19: 37-38

- Gross CG (1991) Contribution of striate cortex and the superior colliculus to visual function in area MT, the superior temporal polysensory area and inferior temporal cortex. *Neuropsychologia* 29: 497-515
- Harris LR, Morgan MJ, Still AW (1981) Moving and the motion after-effect. *Nature* 293: 139-141
- Hlavacka F, Mergner T, Bolha B (1996) Human self-motion perception during translatory vestibular and proprioceptive stimulation. *Neuroscience Letters* 210: 83-86
- Hulk J, Jongkees LBW, (1948) The normal cupulogram. *Journal of Laryngology* 62:70-75
- Ivry RB, Keele SW (1989) Timing functions of the cerebellum. *Journal of Cognitive Neuroscience* 1: 136-152
- Ivry RB, Diener HC (1991) Impaired velocity perception in patients with lesions of the cerebellum. *Journal of Cognitive Neuroscience* 3: 355-365
- Jian BJ, Shintani T, Emanuel BA, Yates BJ (2002) Convergence of limb, visceral, and vertical semicircular canal or otolith inputs onto vestibular nucleus neurons. *Experimental Brain Research* 144: 247-257
- Jongkees LBW (1974) Pathology of vestibular sensation. In: Kornhuber HH (ed.) Vestibular system: Psychophysics, applied aspects and general interpretations (Handbook of sensory physiology) Springer-Verlag, New York pp 413-450
- Jurgens R, Boss T, Becker W (1999) Estimation of self-turning in the dark: comparison between active and passive rotation. *Experimental Brain Research* 128: 491-504
- Koenderink JJ (1990) Some theoretical aspects of optic flow. In: Warren R, Wertheim AH (eds) Perception and control of self-motion. Erlbaum, London, pp 53-68
- Kuno S, Kawakita T, Kawakami O, Miyake Y, Watanabe S (1999) Postural adjustment response to depth direction moving patterns produced by virtual reality graphics. *Japanese Journal of Physiology* 49: 417-424
- Lund S (1980) Postural effects of neck muscle vibration in man. *Experientia* 36: 1398

- Lund S, Broberg C (1983) Effects Of Different Head Positions On Postural Sway In Man Induced By A Reproducible Vestibular Error Signal. *Acta Physiologica Scandanavia* 117: 307-309
- Marple SL (1987) Digital Spectral Analysis. Prentice-Hall,
- Mesland BS, Finlay AL, Wertheim AH, Barnes GR, Morland AB, Bronstein AM, Gresty MA (1996) Object motion perception during ego-motion: patients with a complete loss of vestibular function vs. normals. *Brain Research Bulletin* 40: 459-465
- Monen J, Brenner E (1994) Detecting changes in one's own velocity from the optic flow. *Perception* 23: 681-690
- Morland AB, Jones SR, Finlay AL, Deyzac E, Le S, Kemp S (1999) Visual perception of motion, luminance and colour in a human hemianope. *Brain* 122: 1183-1198
- Nakamura T, Bronstein AM (1995) The Perception of Head and Neck Angular Displacement in Normal and Labyrinthine-Defective Subjects - A Quantitative Study Using A Remembered Saccade Technique. *Brain* 118: 1157-1168
- Pavard B, Berthoz A (1977) Linear acceleration modifies the perceived velocity of a moving visual scene. *Perception* 6: 529-540
- Pelah A, Barlow HB (1996) Visual illusion from running. *Nature* 381: 283
- Pelah A, Secker B, Bishop A, Askham C (1998) A wide-field simulator for studying visuo-motor interactions in locomotion. *Journal of Physiology* 506: 12P
- Pelah A, Boddy A (1998) Adaptive modulation of the motion after-effect by walking. *Journal of Physiology* 506: 111P
- Pelah A, Thurrell AEI, Berry M (2001) Reduction of perceived visual speed during locomotion: Evidence for quadrupedal perceptual pathways in human? *Journal of Vision* 1: 307a URL <http://www.journalofvision.org/1/3/307/>
- Previc FH, Mullen TJ (1991) A comparison of the latencies of visually induced postural change and self-motion perception. *Vestibular Research* 1: 317-323

- Probst T, Brandt T, Degner D (1986) Object-motion detection affected by concurrent self-motion perception: Psychophysics of a new phenomenon. *Behavioural Brain Research* 22: 1-11
- Read HL, Siegel RM (1997) Modulation of responses to optic flow in area 7a by retinotopic and oculomotor cues in monkey. *Cerebral Cortex* 7: 647-661
- Rodman HR, Gross CG, Albright TD (1990) Afferent basis of visual response properties in area MT of the Macaque. II. Effects of superior colliculus removal. *Journal of Neuroscience* 10: 1154-1164
- Roll JP, Vedel JP, Roll R (1989) Eye, head and skeletal muscle spindle feedback in the elaboration of body references. *Progress in Brain Research* 80: 113-123
- Royden CS, Banks MS, Crowell JA (1992) The perception of heading during eye movements. *Nature* 360: 583-585
- Sahraie A, Milders M, Niedeggen M (2001) Attention induced motion blindness. *Vision Research* 41: 1613-1617
- Shenoy KV, Bradley DC, Andersen RA (1999) Influence of gaze rotation on the visual response of primate MSTd neurons. *Journal of Neurophysiology* 81: 2764-2786
- Stoerig P, Cowey A (1997) Blindsight in man and monkey. *Brain* 120: 535-559
- Stoffregen TA (1985) Flow structure versus retinal location in the optical control of stance. *Journal of Experimental Psychology* 11: 554-565
- Stone LS, Perrone JA (1997) Human heading estimation during visually simulated curvilinear motion. *Vision Research* 37: 573-590
- Thurrell AEI, Pelah A, Distler HK. (1998) The influence of non-visual signals of walking on the perceived speed of optic flow. *Perception* 27: 147.
- Thurrell AEI, Bertholon P, Bronstein AM (2000) Reorientation of a visually evoked postural sway response during passive whole body rotation. *Experimental Brain Research* 133: 229-232

- Tootell RB, Reppas JB, Dale AM, Look RB, Sereno MI, Malach R, Brady TJ, Rosen BR (1995) Visual motion aftereffect in human cortical area MT revealed by functional magnetic resonance imaging. *Nature* 375: 139-141
- Turano KA, Heidenreich SM (1996) Speed discrimination of distal stimuli during smooth pursuit eye motion. *Vision Research* 36: 3507-3517
- Turano KA, Heidenreich SM (1999) Eye movements affect the perceived speed of visual motion. *Vision Research* 39: 1177-1187
- van den Berg AV, Beintema JA (1997) Motion templates with eye velocity gain fields for transformation of retinal to head centric flow. *Neuroreport* 8: 835-840
- von Helmholtz H (1896) The direction of vision. In: Southall JPC (ed) *Handbuch der Physiologischen Optik* Vol. 3. Optical Society of America, pp 242-281
- Warren WH, Hannon DJ (1988) Direction of self-motion is perceived from optical flow. *Nature* 336: 162-163
- Wertheim AH (1994) Motion perception during self-motion: the direct versus inferential controversy revisited. *Behavioral and Brain Sciences* 17: 293-355
- Wickens CD (1980) The Structure of Attentional Resources. *Attention and Performance* 8: 239-257
- Wolsley CJ, Buckwell D, Sakellari V, Bronstein AM (1996) The effect of eye/head deviation and visual conflict on visually evoked postural responses. *Brain Research Bulletin* 40: 437-442
- Wolsley CJ, Sakellari V, Bronstein AM (1996) Reorientation of visually evoked postural responses by different eye-in-orbit and head-on-trunk angular positions. *Experimental Brain Research* 111: 283-288

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.

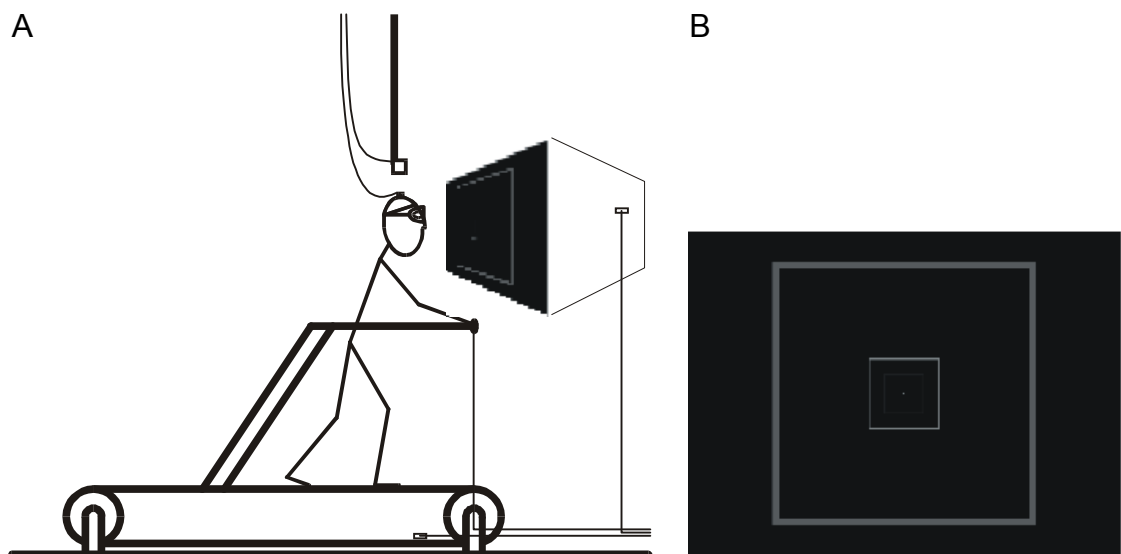


Figure 1 a) The experimental set-up, subjects wore stereoscopic occluding goggles and the head tracking receiver at all times. b) Reconstructed screen-shot of the tunnel.

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

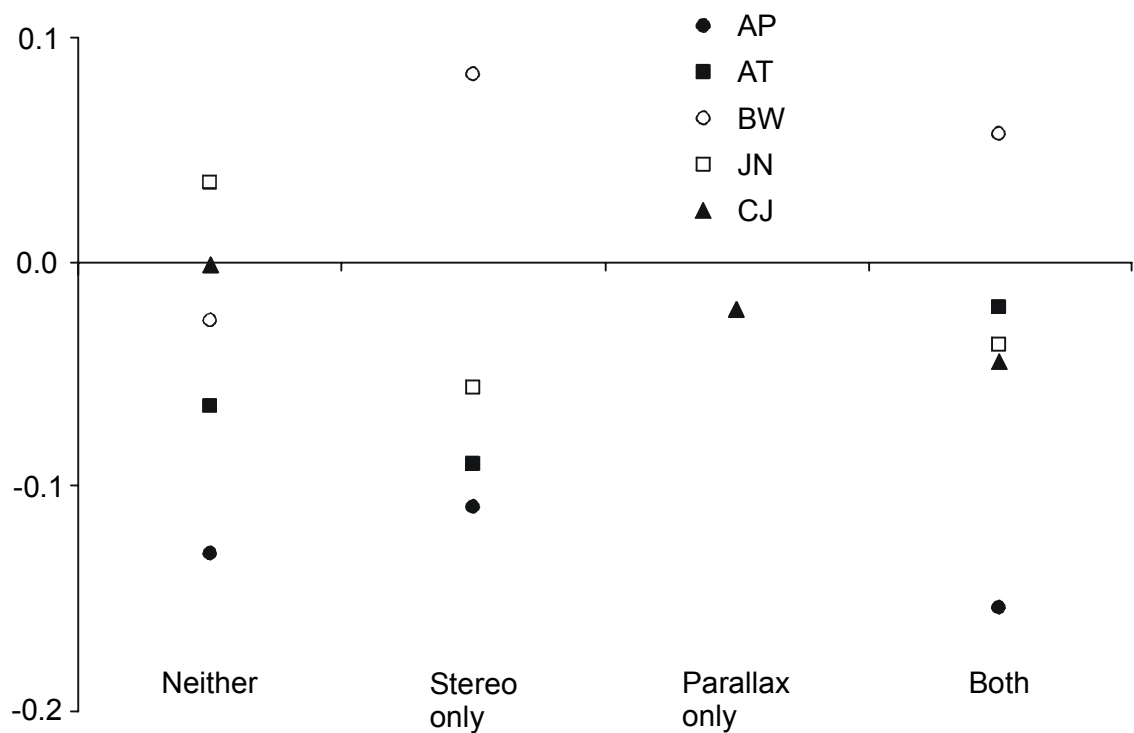


Figure 2 Effect strengths as measured by the slope of the line of best fit between perceived tunnel speed plotted against walking speed for each subject. All subjects were tested in the control and full 3D conditions, with subjects AP, AT, BW and JN also tested in the stereo only condition and subject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