Optic flow, egocentric direction and walking.

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Abstract

This research explored two aspects of visually guided walking; (1) what is the role of optic flow in the recalibration of misperceived direction while walking, and (2) how does a change in perceived direction map onto a change in walking direction.

Data from five studies investigating adaptation to displaced direction (by prism glasses) suggested the following. First, optic flow is important in the recalibration of perceived direction. Further, processing optic flow is attentionally demanding, such that when cognitive load is increased, recalibration decreases. The results also demonstrated that the timecourse of recalibration changed as a function of the presence, or absence, of optic flow.

With regards to the relationship between egocentric direction and walking direction, we demonstrated that a change in visual straight ahead could be mapped onto a change in target-heading error. We found that this relationship held when we unpacked the data according to the direction of displacement to which observers were exposed. The important relationship between visually perceived direction and walking direction was also highlighted in a patient study, using patients whose perception of direction was endogenously shifted after a right hemisphere stroke.

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direction, and that change in perceived visual straight ahead can be mapped onto a changed in walking direction.

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DECLARATION

This work has not previously been accepted in substance for any degree and is not concurrently submitted in candidature for any degree.

Signed .... (candidate) Date 7th Dec 2010

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This thesis is being submitted in partial fulfilment of the requirements for the degree of PhD.

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This thesis is the result of my own independent work/investigation, except where otherwise stated.
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the roof of the lecture theatre to pick up my recordings of perceived straight ahead that blew away in the wind. In addition I am immensely thankful to my participants who persevered with the cold, and often wet and windy weather.

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Table of Contents

List of Figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

Chapter 7

Chapter 8

List of Tables

Chapter 6

Chapter 7

Introduction

If you wish to catch an object (Le Seac'h, Senot, & McIntyre, 2009), reach for an object (Goodale, 2005; Kelly & McNamara, 2009), throw an object (Martin, Keating, Goodkin, Bastian & Thach, 1996), or walk towards an object (Rushton, Harris, Lloyd & Wann, 1998), you need to know the position of the object relative to your body – you need to know its egocentric position. However, one problem with using this source of information is that it tends to drift, and there are several instances when successful action depends on being able to modify, or recalibrate the relationship between signals and judged egocentric direction.

Consider reaching for an object that you are currently fixating. The geometrical position of the object is specified by the orientation of your eyes in your head and the orientation of your head on your body. Thus, to successfully reach for the object your eye-head, and head-shoulder, signals should be accurately calibrated, yet there is evidence to suggest that these signals can drift. For example, Paap and Ebenholtz (1976) revealed that sustained fixation of gaze to one side led to a drift in perceived direction. Figure 1.1 shows a summary of their data.

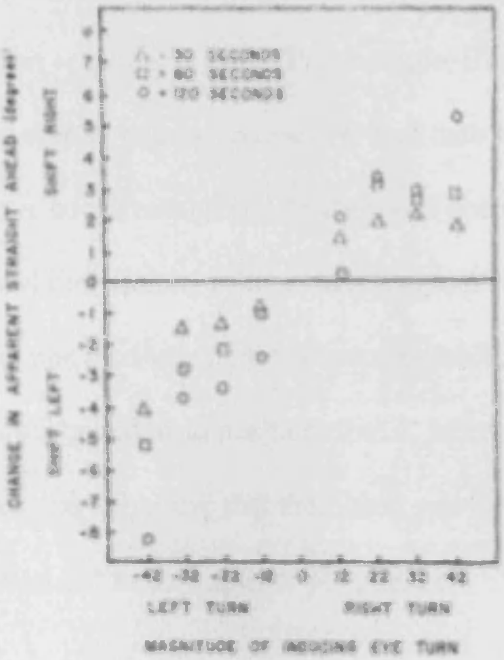

Figure 1.1. Results of Paap and Ebenholtz (1976). Illustrates observer's perceived straight ahead after previously fixating their gaze off to one side. Observers were required to fixate for a period of 30, 60 or 120 seconds at one of four eccentricities either to the left or right side of space.

To measure a drift in perceived direction observers were required to adjust the position of an LED until it appeared to be straight ahead of them, both prior to and after turning their eyes to one side. The results of Paap and Ebenholtz (1976) highlight that after observers fixated their gaze leftwards, perceived straight ahead (a primary axis of egocentric space) drifted to the left. The same also applied to a rightward fixation – perceived straight ahead drifted to the right. The magnitude of the drift was found to be a function of the duration and eccentricity of the observer's fixation.

Similar deviations have also been found for perceived direction in relation to the torso after holding the head in an eccentric posture. For example, Howard and Anstis (1974) demonstrated that merely having an observer turn their head to one side induced a shift in hand-eye coordination. Unlike Paap and Ebenholtz, Howard and Anstis measured perceived direction by asking observers to point straight ahead with both index fingers. Using this measure, perceived straight ahead was found to shift in the same direction as the sustained head position: that is, when physically positioned straight ahead observers came to believe that their head was rotated 6° to the right after holding it in a position 24° to the right for 10 minutes.

Next, consider a developmental problem for egocentric direction distance perception. If you fixate an object of interest the vergence angle provides a source of information about the distance of the object relative to your head. As an infant grows, the interocular distance increases, and so the mapping between vergence angle and distance changes.

The relationship between sensory signals and egocentric position also change every time you put on, or take off, glasses or contact lenses. For first time wearers objects within the environment often look odd, or the eyes feel strange, even though vision is actually much clearer than what it once was. This is often the result of the prescription forcing the eye to adopt a different gaze direction in order to fixate an object: the new lenses change both the vergence angle of an object of interest and also the relative disparities (see Figure 1.2). However, after a short period of time, most wearers simply 'get used to' (adapt to) their new prescription.

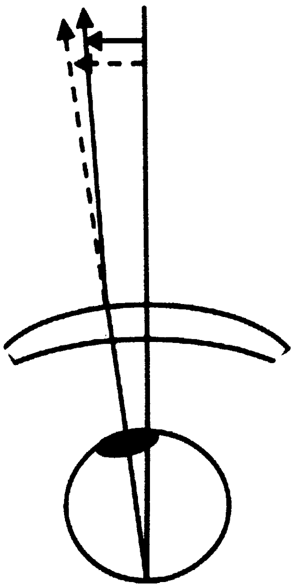

Figure 1.2. Illustration of eccentric gaze through a spectacle lens. The cross-section of a plus lens is shown such that the lens is thicker in the centre – similar to two prisms positioned base to base. The dashed arrows indicate where the observer would previously look to fixate an object; the solid arrows indicate the change in gaze direction induced by the prescribed lens. Due to the variation in the width of the lens this change in eye direction varies as a function of eye eccentricity.

Finally, consider the environment: swift changes in environmental conditions and external forces, such as windy weather, require an observer to adjust their movement plan. Perceptual environments such as those experienced by astronauts (Bock, 1998) or deep-sea divers (Ross & Lennie, 1971; Wells & Ross, 1980) also contain discrepant information that must be recalibrated for accurate motor performance. For example, the lack of gravitational muscle loading experienced by astronauts can cause sensorimotor discordance such that aimed movements are considerably impaired (Bock, 1998). For deep-sea divers, due to the refraction of light through the air, water, and glass of the facemask, depth perception is impaired such that underwater objects are perceived to be about one quarter closer to the observer (Ross & Lennie, 1971). In both circumstances however, individuals are able to adapt quite well to the discordant sensory information (Bock, 1998; Ross & Lennie, 1971).

Given that accurate estimations of egocentric position are important for the visual guidance of action, the brain must be able to adapt, or recalibrate, when there is a drift, or a change in the mapping between different sensory systems. In this thesis, I will examine the role of visual information in the recalibration process, focusing specifically on the recalibration of egocentric direction in the walking observer. I will first start with a brief overview of how walking may be visually guided before moving on to the crux of the thesis by providing a concise review of the literature that is concerned with recalibration.

Information for the visual guidance of walking

The following is a brief summary of the debate concerned with what visual information is used to guide locomotion. Although this is not the main focus of the thesis, the reader will benefit from an overview of the topic.

Sixty years ago Gibson (1950) proposed the revolutionary idea that humans rely on optic flow[1] for the visual guidance of locomotion. Gibson noted that when travelling

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[1] In the tradition of Gibson, up to present day (e.g. Bruggeman & Warren, 2010) we describe the motion information available to the moving observer in terms of the optic flow field (the expanding pattern of motion produced at the eye). The true definition of optic flow is ambiguous, and can consist of several aspects including motion parallax, translational motion, and planar motion, as well as the focus of expansion. Because humans typically use eye and head movements to scan the scene or maintain fixation on a scene object, the flow field on the back of the eye will not be the optic

on a straight path an observer experiences a pattern of visual motion that radially expands out of a singular point along the direction of heading. The point from which motion is perceived to radiate was termed the focus of expansion (FoE). Gibson contended that by localising the FoE, and aligning it with a target, an observer can steer towards his or her goal. Gibson's proposals stimulated a vast amount of subsequent research concerned with the role of optic flow in the visual guidance of locomotion – most notably Bill Warren and collaborators (e.g. Warren, Morris and Kalish, 1988; Fajen & Warren, 2000) champion the optic flow hypothesis.

Self-motion throughout a natural environment is usually accompanied by eye movements and head movements: for example, Beverley and Regan (1982) highlighted that if an observer were to look at some point within the environment other than their target of interest, the FoE would coincide with their gaze direction and not the direction of heading. Under such circumstances it has been proposed that walking direction in a structured environment can be specified by motion parallax between objects at different depths, or by using extraretinal signals pertaining to the direction of gaze (see Warren, 2007). In addition, Llewllyn (1972), and more recently Wilkie and Wann (2003), proposed that heading direction can be determined by referring to the position of objects within the environment relative to the observer. More specifically, if an observer is walking on a straight path the position of objects within the environment will remain fixed relative to their egocentric position, if,

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flow field, but the sum of optic flow and laminar flow due to gaze rotations. Very extensive psychophysical research on judgments of self-movement from optic flow indicates observers can use extra-retinal information to compensate for eye (e.g. Royden, Banks & Crowell, 1992) and head (Crowell, Banks, Shenoy, Andersen, 1998) rotations. We direct the reader to the extensive work by Freeman (e.g. Freeman, Champion, Sumnall, & Snowden, 2009; Souman & Freeman, 2008) for a review of how retinal and extra-retinal signals are combined.

however, an observer is walking on a curved path, objects will appear to drift from their fixed position.

Rushton, Harris, Lloyd and Wann (1998) questioned the role of optic flow in the visual guidance of walking and proposed a heuristic that is conceptually related to Llewellyn's (1972) drift hypothesis, but is different in important ways. The egocentric direction account of locomotion (Rushton et al. 1998) also focuses on the direction of a target measured relative to the centre of the trunk (the ego-centre). With drift cancellation (Llewellyn, 1972) the direction of the first step will determine the whole trajectory; however, according to the egocentric direction theory, an observer will reach their target by continuously making a corrective action to realign their body with the target object if it drifts from the centre of their trunk while walking – observers always attempt to keep the target at a fixed egocentric position (usually straight ahead). To dissociate an optic flow strategy from egocentric direction Rushton et al. used prism glasses. While wearing prisms the direction of a target positioned straight ahead relative to the observer will be perceived as either to the left or right of the individual's mid-line, depending on the base of the prism. Optical relationships within the field of view remain undisturbed. Consequently differential properties of the optic flow field, such as FoE alignment with the target, remain unaltered, even though they are displaced. Thus, if observers use optic flow they should take a straight path towards the target; if observers use egocentric direction one would expect an indirect, curved trajectory, as observers attempt to navigate towards the displaced location and not the actual location of the target.

In line with the egocentric direction theory, while wearing displacing prisms, participants did indeed follow the predicted curved trajectory to the target object. The results of Rushton et al. have now been replicated and extended by several research groups, with many championing the egocentric direction strategy over optic flow as the fundamental cue to heading perception (e.g. Rogers & Allison, 1999; Rogers & Dalton, 1999; Harris & Carre, 2001; Harris & Bonas, 2002). However, the optic flow vs. egocentric direction debate continues (e.g. Fajen & Warren, 2000; Warren, Kay, Zosh, Duchon, & Sahuc, 2001; Rushton, 2008)

Researchers investigating adaptation during walking have generally taken an agnostic position with regards to what visual information is used to guide walking (e.g. Redding and Wallace, 1997). Similarly, the primary aim of this thesis is concerned with the investigation of the role of optic flow in *recalibration* while walking and not the visual *guidance* of walking. Although this brief overview is provided here for the purpose of completeness, the assumptions of the egocentric direction theory are relevant, particularly in Chapter 6.

The recalibration of egocentric direction: Held's reafference model

The most notable research with regards to the recalibration of egocentric space was inspired by the "reafference principle" *(Das Reafferenzprinzip)* developed by von Holst and Mittelstaedt (1950), and von Holst (1954). The principle states that an organism is able to distinguish between visual changes that are due to self-movement (reafference), and visual changes that are due to movement within the environment (exafference), by making use of information about self-generated action (efference copies).

Held (1961; Held & Hein, 1958) expanded von Holst's (1954) model by adding a new component that he referred to as 'correlation storage' (see Figure, 1.3). Similar to a memory store, Held suggested that correlation storage is used to hold previous combinations of concurrent efferent (a neural reproduction of a motor movement) and reafferent signals. Over time an observer will learn that a particular form of reafferent visual input accompanies a particular motor movement. This one-to-one relationship between perception and action is then stored in correlation storage. A discrepancy is detected when the incoming efferent and *reafferent* signals do not match those that are held in correlation storage. As a consequence of this discrepancy, an error signal is generated indicating that correlation storage must be reprogrammed (recalibrated) to match the new signal combinations.

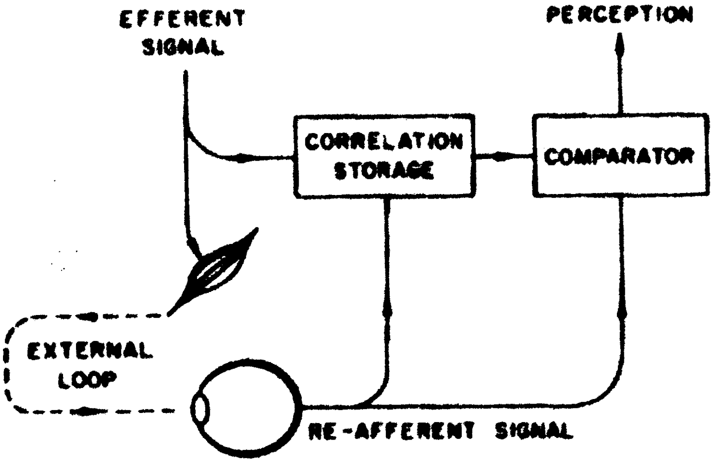

Figure 1.3. Illustration of Held's reafference model. Taken from Held (1961). When a particular motor movement is initiated a neural reproduction (efferent signal) is emitted that is then held in 'correlation storage' with a visual signal (reafference).

The development of such correlations between motor and visual information allows predictions to be made with regards to expected reafference. According to Held, the current reafferent signal is sent directly to the comparator as well as to correlation storage. Based on the particular motor movement (efferent signal), correlation storage sends the anticipated visual (reafferent) signal to the comparator. Within the comparator the two reafferent signals (the experienced signal and the expected signal) are compared. If there is a mismatch between current and anticipated reafference an adaptive process is initiated such that new correlations are formed between efferent outputs and reafferent inputs.

Held (1961) suggested that active movement was necessary for recalibration to occur since, in his model, reprogramming is based on discordant reafferent information – the feedback signal that is correlated with self produced movement. Indeed, active and passive movement can be perceived quite differently: for example, an active eye does not usually yield an impression of world movement, whereas a passively moved eye does. There are some historical antecedents to Held who also stressed the importance of active movement in adaptation to a misperception of direction (e.g. Stratton, 1897; Wooster, 1923). However, Held was the first to explore the role of active movement using systematic empirical experiments that set the standard for measuring recalibration.

The basic procedure used by Held to measure recalibration involved a period of exposure to discordant information with quantitative before and after measurements. To inject an error into perceived direction Held used wedge prisms to rotate the visual scene relative to the observer, displacing the apparent position of objects in the visual array (Figure 1.4 A B). To determine the magnitude of recalibration Held and Gottlieb (1958) presented observers with the image of a set of targets reflected by a mirror. The task required them to reach under the mirror to a concealed surface and mark the perceived location of the targets (see Figure 1.4 C). To gain an open loop measure of recalibration the task was performed without feedback – the observer was unable to view his/her hand, or the marks made, and thus was unable to correct for any errors. This task was performed both prior to and after exposure to the prisms. Differences in task performance from pre- to post-exposure were taken as an indication of recalibration. In general, the exposure period involved one of three conditions: observers viewed their hand through laterally displacing prisms while it was (i) motionless, (ii) moved actively, or (iii) moved by the experimenter while in a relaxed state (passive condition).

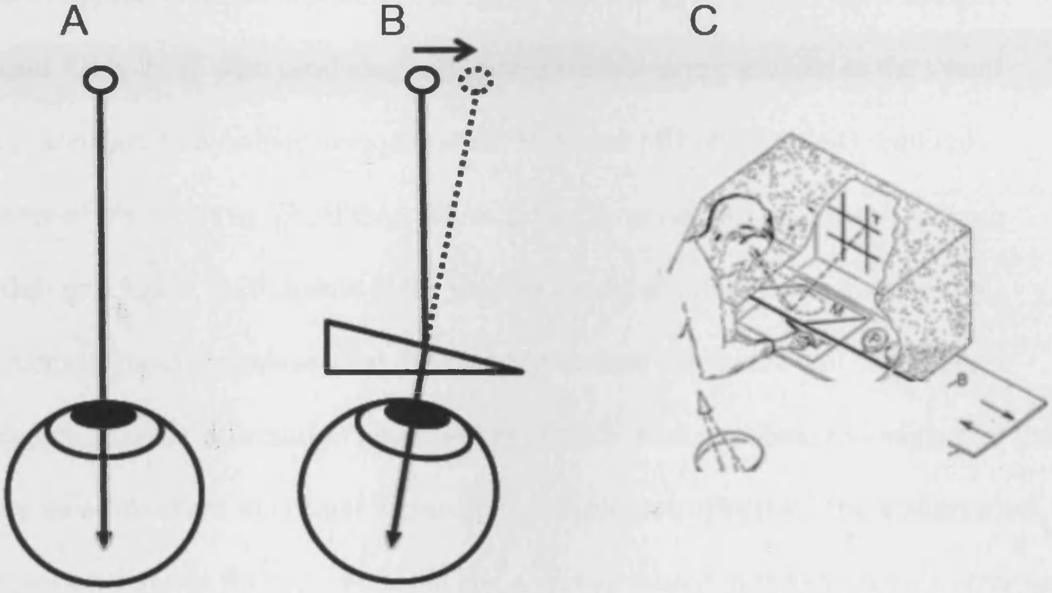

Figure 1.4. Schematic representation of (A) viewing a distant target in the absence of prisms; (B) viewing a distant target through base left, rightward displacing prisms; (C) the apparatus developed by Held and Gottlieb to measure recalibration after exposure to prisms (misperceived direction). Taken from Held and Gottlieb (1958).

Using the Held and Gottlieb paradigm the reafference hypothesis was initially supported by several studies demonstrating that adaptation to a misperception of direction required active movement (Held & Gottlieb, 1958; Held & Hein, 1958; Held & Schlank, 1959; Held & Freedman, 1963). However, this work predominantly focussed on the recalibration of eye-hand coordination using pointing movements. Held later switched to a walking exposure paradigm to investigate the role of active movement in the walking observer.

Held and Bossom (1961) had observers wear laterally displacing prisms while they either actively walked or were passively pushed in a wheelchair along the same path. To measure recalibration under these exposure conditions observers were seated and were required to rotate themselves so that a visual target appeared to be straight ahead. Only those who produced self-generated movement adapted to the visual displacement. In a further demonstration, Held and Mikaelian (1964) required 'passive' observers to wheel themselves along the same path as 'active' walking observers. Again, participants in the passive condition did not demonstrate any perceptual motor compensation. Held and Mikaelian concluded that adaptation requires efferent information generated by specific motor actions, and suggested that only those involved in normal locomotor behaviour are effective. The authors also suggested that this finding overcame any criticism related to the passive observer not being motivated to attend to the visual feedback, or make decisions based upon the discrepant information.

In the case of the walking observer Held and Freedman (1963) suggested that optic flow is the most important source of reafferent visual information for the recalibration of misperceived direction. Held suggested that a given locomotor movement would yield a characteristic pattern of optic flow: that is, there is a one-to-one relationship between an observer's movement and the corresponding flow pattern. For example, while walking under normal circumstances an observer would experience an optical flow pattern whereby the centre of the flow field (the FoE, where there is an absence of visual motion) coincides with the target object to which they are heading. However, if direction is misperceived the pattern of visual motion will be reciprocally affected (see Figure 1.5). Recalibration in the walking observer is prompted when there is a discrepancy between the anticipated and perceived pattern of reafferent visual motion (Held & Freedman, 1963).

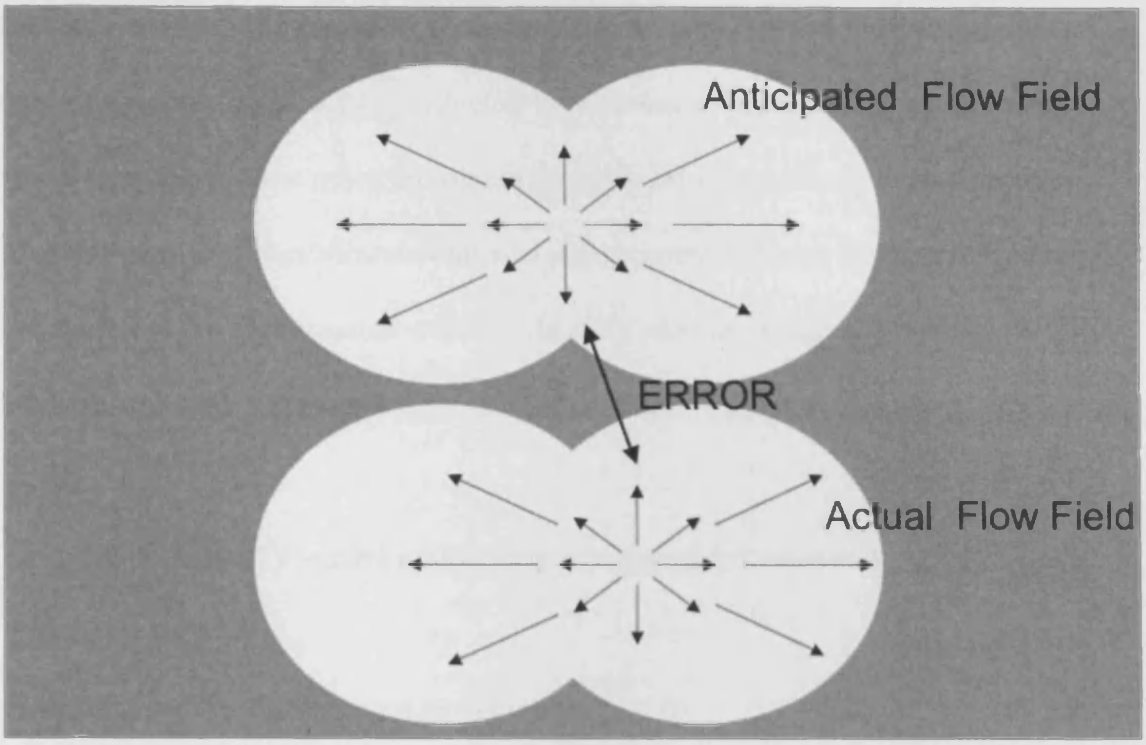

Figure 1.5. The point from which motion is perceived to radiate is termed the focus of expansion (FoE). Gibson (1958) contended that by localising this point and aligning it with a target an observer could steer towards his or her goal. Held and Freedman (1963) suggested that if there is a discrepancy between the expected pattern of visual motion (top panel – aligned with the direction of heading) and the perceived pattern of visual motion (lower panel – displaced FoE) then this produces an error signal which in turn drives a recalibration of perceived direction.

The results of an experiment conducted by Mikaelian and Held in 1964 are consistent with a role for optic flow in the recalibration of perceived direction. As in previous experiments, Mikaelian and Held measured the magnitude of recalibration in passive (wheelchair pushed) and active (self-produced locomotion) observers. Two different environments were used: one consisted of a hallway to provide a structured visual array. A second environment decreased structure by exposing observers to dimly lit spheres hung at random positions in a dark room. Reducing the structure of an environment can be likened to reducing the saliency of optic flow: the richer the visual environment the more prominent the optic flow. In both settings the active observer exhibited recalibration that was significantly different from zero. However, the magnitude of recalibration was significantly reduced in the unstructured environment highlighting the prominent role of optic flow.

Evaluation of Held's model and review of subsequent research

The necessity of self-generated movement

Held's argument for the necessity of active movement is not without its critics. For example, when discussing Held and Bossom's (1961) work, Howard and Templeton (1966) contended that the conclusion with regards to reafference being a necessary condition for adaptation was not justified, suggesting that the authors "unwittingly biased their experimental situation in favour of their hypothesis [and]... they should have concluded that reafference is sufficient rather than necessary for visual-motor coordination" (p285). The bias that Howard and Templeton refer to concerns Held's measures of recalibration: the target task shown in Figure 1.3 C, and the task used after walking exposure (turning to face a visual target) both involved active movement and so were biased towards this form of recalibration. For passive observers, it may have been more appropriate to include a passive measure of recalibration; for example, rather than ask the observer to move their own arm, it could be moved by the experimenter until the observer is satisfied that it was in the correct position.

Many studies that followed Held were unable to replicate his findings with regards to the necessity of self-generated movement. For example, Weinsten, Sersen and Weinsten (1964), Singer and Day, (1966) and Mather and Lackner (1981) all found quite robust adaptation with passive movements, yet the general trend did suggest that active movements tended to facilitate adaptation. Wallace and Garret (1973; 1975) measured recalibration in hypnotised observers who were given the suggestion that their arms were "absent from all sensations" (p598). Their results revealed that active movement of the arm did not produce any adaptation when the arm was hypnotically anesthetised, suggesting that active movement does not always guarantee adaptation. However, all of these experiments are concerned with pointing exposure and not walking exposure. Few experiments have dealt with the active vs. passive debate using a walking exposure paradigm. In one experiment, however, Quinlan (1970) was able to replicate Held's walking findings, yet this was only the case when the passive observer was prevented from viewing their body.

Held (1968) subsequently recognised some of the limitations of his early position, stating that "active movement with its accompanying sensory feedback is an essential condition for adaptation under circumstances in which no other important source of error information is available" (p57). It is now generally accepted that active movement may not be a necessary condition for recalibration.

The type of visual reafferent information

Held's model (Held, 1961; Hein & Held, 1961; Held & Freedman, 1963) suggests that reafferent visual information is key in prompting perceptual-motor recalibration. However, historically this has not always been thought to be the case. Over 300 years ago in his famous *"Essay toward a new theory of vision"* Berkeley (1963, originally published in 1709) suggested that touch recalibrates (or 'educates') vision. Indeed, there are examples in more recent research that visual exposure to an optical displacement is not enough to recalibrate direction. For example, Howard, Craske and Templeton (1965) exposed observers to rotated vision through a series of mirrors. In one condition observers watched a long wooden rod mounted horizontally in line with their saggital plane as it moved away from, and then towards them, so that it touched the observer centrally on the lips. For a second group of observers, exposure conditions remained the same except the moving rod did not have physical contact. Significant adaptation was only found in the 'touch' condition suggesting that contact with the mouth informed the observer that the rod was not where it appeared to be.

However, there are several lines of evidence that point to vision, and not touch, as being the primary source of information used in the recalibration of direction in the walking observer. Indeed, the results of Mikaelian and Held (1964) highlight optic flow as playing an important role in the recalibration of perceived direction while walking. Rock (1966), however, suggested a different form of reafferent visual information, advocating 'target drift' as an alternative to a shift in the FoE.

Rock (1966) suggested that the viewed position of an object, and perceived movement of the object in relation to an observer, might provide a good source of information to enable the recalibration of perceived direction. For example, if an object is straight ahead of a walking observer, it will remain straight ahead if the observer takes a straight trajectory towards it. In contrast, if the object is not straight ahead of the observer then its direction will change on each step and the position of the object will appear to ‘drift’. Rock suggested that an observer may use this ‘target drift’ to recalibrate perceived direction (Figure 1.6).

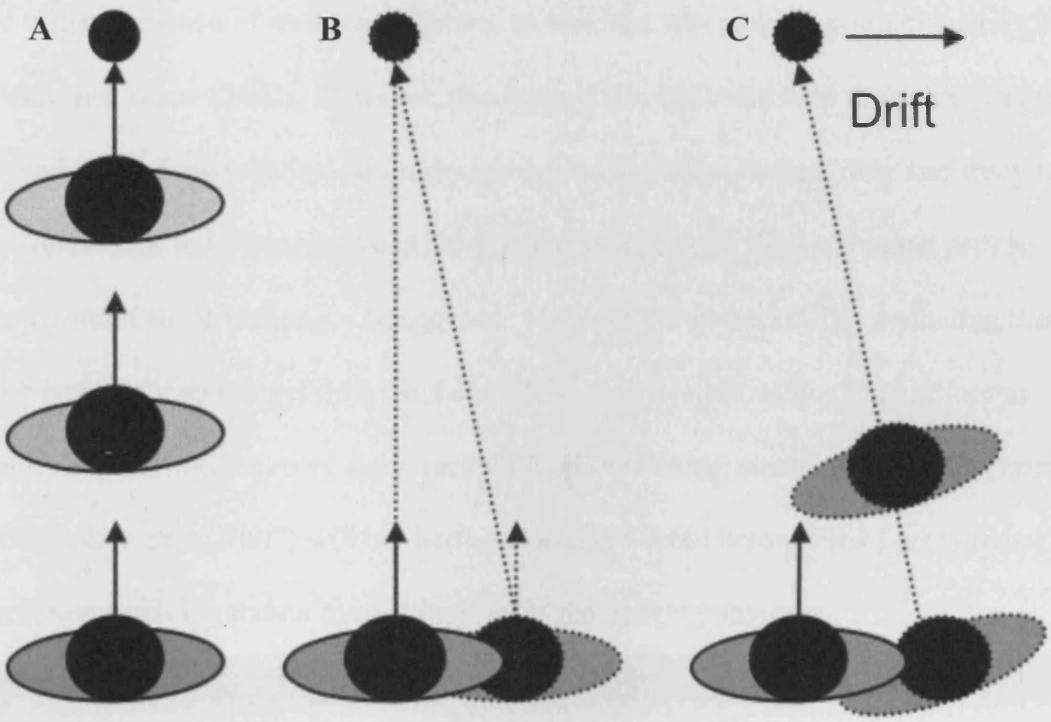

Figure 1.6. Illustration of Rock’s (1966) target drift hypothesis to highlight the role of visual information in the recalibration of perceived direction. A: if an observer has a true perception of direction and the target is located straight ahead then the target will not appear to drift when walking towards it, and the observer will take a straight path. B: if an observer has a misperception of direction such that perceived straight ahead has drifted to the right (dotted outline) then the straight-ahead target will appear to be to the left of the observer. C: to reach the target the observer will turn leftwards to walk towards it. As the observer walks towards the target it will appear to drift to the right. Rock suggested that perceived direction could be recalibrated by nulling any drift in target location.

Although Rock's theory provides an interesting alternative with regards to the type of reafferent visual information that drives recalibration of perceived direction, little research has been conducted in relation to this hypothesis. As previously discussed, Llewellyn (1971) later proposed that target drift can be used as an online strategy for the visual guidance of walking direction, an idea that was picked up more recently by Wilkie and Wann (2003). However, this research is concerned with the online control of walking and not recalibration of misperceived direction. Indeed, only one study to my knowledge has tested between the involvement of optic flow and target drift in recalibration while walking – Bruggeman, Zosh and Warren (2007), concluding that both optic flow and target drift can be used for recalibration, although exposure to optic flow allowed for more rapid recalibration of walking direction. This experiment (Bruggeman et al., 2007) will be discussed in more detail below. First I will discuss earlier research in relation to recalibration in the walking observer.

The work of Redding and Wallace

Throughout the 1970s and 1980s Gordon Redding and Benjamin Wallace conducted a series of seminal experiments with regards to recalibration in the walking observer. Following on from Held's research, Redding and Wallace (1997) assumed that the minimum requirement for recalibration is that the observer is provided with some form of information as to the nature of a discrepancy between sensorimotor systems. However, although they do not comment on the specific nature of this 'information' they do state in their later papers that they do not believe it to be optic flow, a suggestion that will be discussed in more detail below.

Similar to Mikaelian and Held (1964), Redding and Wallace used university hallways as their laboratory setting in all of their walking experiments, and incorporated the use of displacing prisms. However, unlike the work of Held, Redding and Wallace measured different forms of recalibration within the perceptual motor system. The nature of the measures is to be discussed in much greater detail in Chapter 2. Briefly, however, Redding and Wallace measured changes within the eye-head system (visual adaptation), and changes in felt limb position (the hand-head, proprioceptive system). In general, while walking, Redding and Wallace found that proprioceptive adaptation was greater than visual adaptation, however a number of factors were found to influence the magnitude of this recalibration.

Redding (1981) found that alternating the exposure environment between two different hallway settings increased recalibration, an effect that he attributed to attention: when exposure conditions are constantly changing attentional processes are required, leading to greater recalibration. In turn, when observers do not remain vigilant as to the discrepancy between sensorimotor systems, recalibration is limited. In order to further investigate the role of attention in recalibration, Redding and collaborators conducted a series of experiments where attentional capacity was manipulated via the use of a secondary cognitive task (Redding, Clarke & Wallace, 1985; Redding & Wallace, 1985a). The results of these experiments suggest that recalibration depended upon a limited capacity cognitive mechanism, such that when attentional resources were depleted the amount of recalibration obtained decreased. Interestingly, this suggests that processing reafferent visual information is attentionally demanding. This finding will be readdressed in Chapter 4.

In a different set of experiments Redding and Wallace (1985b) found that asking observers to walk faster, did not significantly affect the amount of adaptation obtained. Based on the hypothesis that increasing walking speed increases the saliency of optic flow, the authors suggested that this finding provided evidence that optic flow is not involved in the recalibration of perceived direction. However, it could be argued that optic flow is not related to recalibration in a graded fashion: that is, it might simply be the case that optic flow information while walking is sufficient for recalibration, and that added information by speeding up the locomotion does not contribute. Indeed, it is likely that the 'saliency' of optic flow cues are not increased at all, or sufficiently enough, by increased walking speed, particularly since the difference in flow speed between a fast and slow walking observer is likely to be very small.

Recent research

Following on from the work of Redding and Wallace, to my knowledge, research concerned with recalibration in the walking observer was absent for almost two decades. Morton and Bastian (2004) revisited the issue. The primary aim of Morton and Bastian's (2004) experiment was to investigate whether recalibration while walking can generalise to other movements, such as reaching, and vice versa. Measures of recalibration included the standard measures of visual and proprioceptive straight ahead used by Redding and Wallace, as well as a reaching and a goal oriented locomotor task. Participants were exposed to laterally displacing prisms as they either walked within boundary lines marked out on a laboratory floor, or made reaching movements to a target. In contrast to the results of Redding and Wallace, and Held and his collaborators, Morton and Bastian (2004) did not find any evidence for a recalibration of perceived visual and proprioceptive direction while walking or while reaching.

However, although standard measures of recalibration did not reveal any adaptation, Morton and Bastian did find some indirect evidence of a change in perceived direction: when monitoring the walking trajectories of participants while exposed to the prisms the authors reported a change in participant's heading direction across trials[2]. Interestingly, the results of Morton and Bastian also revealed that adaptation while walking generalised to reaching, yet the reverse relationship was not found. The lack of generalisation from reaching to walking was suggested to be a result of the limited body segments involved in the pointing exposure task.

To test between the role of optic flow and target drift in the recalibration of direction while walking, Bruggeman, Zosh and Warren (2007) used head mounted displays, and not prism glasses, to introduce an error in perceived direction. Participants were required to walk in one of two virtual environments: one textured environment and a second that included only a simple post. Although the presence of a target in both environments meant that target drift was always available, the textured environment was used to enhance the saliency of optic flow, whereas the target environment minimised optic flow. Walking trajectories were monitored while observers walked towards a virtual target displaced 10° to the right. A change in head orientation in

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[2] To illustrate the role of egocentric direction in the visual guidance of walking, Rushton et al. (1998) demonstrated that when perceived direction was displaced walking direction was similarly affected: observers approached a target with a constant bearing angle producing a curved walking trajectory in the form of an equiangular spiral. A change in walking direction can thus be taken as indirect evidence of a change in perceived direction (or recalibration).

relation to the target object across trials was used to indicate a recalibration of perceived direction.

The results demonstrated that, although head orientation was not found to significantly change across trials, target-heading error did decrease across trials in both environments; however, this change was significantly greater in the 'optic flow' environment. This result implies that, as Rock (1966) suggested, target drift does play an important role in the recalibration of direction, yet recalibration is faster in the presence of optic flow. Importantly, however, since the authors were unable to find a significant change in head orientation across trials, Bruggeman et al. (2007) contended that the change in walking direction did not represent a change in perceived direction. Instead, they contended that it signified a recalibration of "visuo-locomotor mappings" (p2038). This is important to note since the literature prior to Bruggeman et al. (2007) – with the exception of Morton and Bastian (2004) – found a change in perceived direction. Thus, although this study provides some interesting results with regards to the roles of optic flow and target drift in the recalibration process, it contrasts with the majority of the previous literature concerned with perceptual motor adaptation in the walking observer. The crucial difference is that Bruggeman et al. used head orientation to measure perceived direction.

In a more recent experiment, Bruggeman and Warren (2010) further investigated the role of optic flow in the recalibration of perceived direction. Unlike their previous experiment, Bruggeman and Warren used the standard pre-test, exposure, post-test design and incorporated several measures of recalibration: head orientation (same as Bruggeman et al. 2007), turning to face a target, throwing a ball, kicking a ball and walking towards a target. Recalibration during the exposure period was measured by a change in walking trajectory across trials. The aim was to test whether recalibration while walking generalised to other goal directed actions. A head mounted display was used to expose observers to either a 10° leftward or rightward displacement. As in the 'optic flow' condition of the previous experiment, observers were required to walk towards a displaced target within a textured virtual environment.

The main finding of the Bruggeman and Warren (2010) paper was that recalibration while walking failed to transfer to the throwing, kicking, or turning to face a target tasks, yet was present when observers were asked to walk towards a target. The authors suggested that optic flow is involved in task-specific recalibration. The lack of transfer of recalibration from walking to other tasks that require egocentric direction was suggested to provide evidence that perceived direction was unaffected. However, this result is surprising given that Morton and Bastian (2004) found that adaptation while walking did generalise to reaching, but not the other way around. In light of these findings one should expected that adaptation while walking should generalise to other behaviours, such as throwing, that require knowledge of egocentric direction.

Similar to Bruggeman et al. (2007), Bruggeman and Warren (2010) did not find a change in head orientation across trials. However, head orientation cannot be described as a pure measure of perceived direction – this measure does not take into account any possible rotation of the head relative to the torso. Asking an observer to point straight ahead, or to move a visual target until it is straight ahead (as used by Held & Bossom, 1961; Redding & Wallace, 1985a; Morton & Bastian, 2004), provides a more accurate representation of perceived direction.

To conclude, with regards to Held's optic flow hypothesis (Held and Freedman, 1963), recent research is inconclusive. Morton and Bastian (2004) were only able to find indirect evidence of a change in perceived direction (change in walking trajectory). However, their exposure task could account for a lack of change in perceived straight ahead – having observers walk within boundary lines, and not directly towards a target, might induce a different form of recalibration. For example, Donges (1978) highlighted that maintaining a constant distance from an edge was not the same as navigating directly towards a target. Bruggeman et al. (2007) also found indirect evidence of recalibration, both when optic flow was present and absent. This result provided indirect evidence that target drift (Rock, 1966) can be used to recalibrate perceived direction, and that the presence of optic flow speeds up the process.

Similar to Morton and Bastian, Bruggeman et al. were unable to find direct evidence of a change in perceived direction, even though (unlike Morton & Bastian) participants were asked to walk towards a target. However, they did not incorporate the standard pre-test, exposure, post-test design used by Held and those who proceeded him (including Redding and Wallace). Although Bruggeman and Warren (2010) did include the standard test design, their results were still confounded by their measure of recalibration. The results of this experiment were also unable to replicate those of Morton and Bastian with regards to the generalisation of walking to other behaviours, such as throwing, which require knowledge of egocentric direction.

Outstanding issues and overview of the thesis

The literature reviewed above highlights that there is a great deal of evidence to suggest that observers are able to recalibrate misperceived direction while walking (e.g. Held & Bossom, 1961; Held & Mikaelian, 1964; Redding & Wallace, 1985a, 1985b, Redding et al., 1985). With regards to Held's idea that self-generated movement is required, many have shown that active movement is neither a necessary, nor sufficient condition for recalibration. Indeed, Held (1968; 2009) later modified his position concerning the importance of active movement.

With regards to the source of visual information that is used to drive recalibration in the walking observer, I described two possibilities: optic flow as proposed by Held and Freedman (1963), and target drift as suggested by Rock (1966). Researchers investigating recalibration while walking have found a change in perceived direction, yet have not sufficiently isolated, or noted the source of reafferent visual information used in the adaptation process. Indeed, it is likely that both optic flow and target drift, in combination with other cues (e.g. environmental cues – Beusmans, 1998; Hahn, Andresen & Saidpour, 2003), play a role in the recalibration of perceived direction. Although the results of Bruggeman et al. (2007) shed some light on how different sources of visual information drive a change in walking direction, they were unable to find direct evidence of a change in perceived direction (standard indication of recalibration).

The question of what source of visual information is used to drive recalibration while walking remains unanswered. The heading direction data of Bruggeman et al. (2007)

suggest that recalibration is faster when optic flow is present, yet is still possible in the absence of optic flow. However, the authors were unable to obtain a change in perceived direction – a finding that is at odds with the previous literature. Possible explanations for this discrepancy may relate to the exposure conditions (Bruggeman et al. used a head mounted display) or the measure used to represent perceived direction (head orientation). In a later experiment, Bruggeman and Warren (2010) did use a pre- and post-test measure of head orientation and still revealed a null effect. It would be interesting to investigate whether using the measures of recalibration developed by Redding and Wallace would reveal a change in perceived direction, and to determine whether this can be mapped onto the change in walking direction found by Bruggeman et al. (2007). Indeed, this is what would be predicted by the egocentric direction account of the visual guidance of locomotion (Rushton et al., 1998). Based on the findings of Bruggeman et al., one could predict that the timecourse of change in perceived direction should be much faster when optic flow is present than when optic flow is absent.

If the timecourse of recalibration can be modified as a function of exposure to different sources of visual information, then the location of recalibration within the perceptual motor system may also vary as a function of exposure to discrepant optic flow or target drift. As mentioned above, Redding and Wallace (e.g. Redding and Wallace, 1985a) found more proprioceptive than visual adaptation. However, optic flow was present in all of their exposure conditions. Thus, it may be possible that recalibration occurs within different perceptual motor systems depending on the presence of optic flow. However, this is a neglected area of research within the literature.

The research of Redding and Wallace (e.g. Redding, 1981; Redding et al., 1985) revealed an interesting result with regards to the role of attention in the magnitude of recalibration. The results suggested that processing discrepant visual information is attentionally demanding, such that when cognitive load is increased, the magnitude of recalibration decreases. Thus, there appears to be a number of factors that can influence the magnitude and occurrence of recalibration with the source of visual information being just one of them. However, the role of other factors is often neglected.

Held (1961; Held & Freedman, 1963) suggested that an error signal (driven by a discrepancy between the anticipated and perceived reafferent visual information) is necessary for recalibration. However, the necessity of an error signal has never been fully elucidated. In all of the above experiments an error signal is present: observer's always experienced target drift or a discrepancy between anticipated and perceived optic flow. What would happen if the same conditions are replicated, but the error signal is removed? Held would suggest that no recalibration should occur. However, this has not been empirically tested.

The presented research has highlighted a gap in the adaptation literature with regards to the role of visual information in the recalibration of direction. This thesis aims to address the outstanding issues outlined above. In five systematic studies the role of optic flow, the sites of adaptation, the necessity of an error signal, the role of attention, the timecourse of adaptation and change in heading error was investigated. All trials took place within the same experimental area, and employed the same standardised methodology that is to be described in Chapter 2. In Chapter 2, I will also introduce the theoretical grounding of the standardised measures of adaptation that are used, and describe how they should be interpreted. I will also address the choice of method used to induce a misperception of direction. In the proceeding three chapters, I will discuss the findings of five empirical studies concerned with perceptual-motor adaptation.

Chapter 3 will consider the role of visual motion in the recalibration of misperceived direction using a number of techniques to both temporally manipulate exposure to optic flow (noflow, experiment 1), as well as spatially manipulating the flow field by reducing observer's field of view (experiment 2). Both visual and proprioceptive adaptation are measured to investigate whether the location of recalibration also varies as a function of the availability of optic flow. In a third experiment, (experiment 3) the role of an error signal is specifically investigated, whereby the conditions of experiment 1 are replicated without the introduction of an optical displacement. This experiment allows clearer conclusions to be made with regards to the role of displaced visual motion in the recalibration of perceived direction: since all else remains equal in this experiment, except for a discrepancy between the anticipated and actual pattern of optic flow, observers should not demonstrate any adaptation.

Chapter 4 explores the effect of cognitive load on the magnitude of recalibration. The results highlight the complexity of the process of perceptual motor adaptation, emphasizing that not only can it be multiply determined, there are other extraneous influences that may prevent it from occurring in the first place. In Chapter 5, I explore the timecourse of recalibration within both the visual and proprioceptive systems when optic flow is continuously, intermittently or not available.

Leading on from this, Chapter 6 examines the relationship between measures of perceived direction and heading direction in the Timecourse experiment. If egocentric direction (Rushton et al., 1998) is, indeed, involved in the visual guidance of walking, then a change in perceived direction should be strongly associated with a change in walking direction. This chapter takes the trajectory results of the Timecourse experiment and thoroughly analyses the relationship between heading error and perceived egocentric direction.

In chapters 3-6, I present the combined adaptation data obtained after exposure to a leftward or rightward rotation of the visual array. In Chapter 7 I investigate another aspect of the exposure situation that might affect recalibration: the difference between displacement direction. This chapter is particularly interesting given that most research looking at adaptation tends to report adaptation as a combination of exposure to both left and rightward displacing prisms (e.g. Foley & Maynes, 1969; Melamed, Halay & Gildow, 1973; Bruggeman & Warren, 2010), or simply use just one displacement direction without providing a justification for doing so (e.g. Singer & Day, 1966; Morton & Bastian, 2004; Bruggeman et al., 2007). However, recently there are hints in the literature to suggest that the magnitude of recalibration after exposure to a left or rightward displacement is asymmetric (e.g. Michel, Vernet, Courtine, Ballay & Pozzo, 2008). Chapter 7 fully describes all asymmetries that exist in the adaptation data obtained in the five adaptation studies. It also highlights a relationship between the asymmetries found in aftereffect measures of adaptation with asymmetries in heading error in the Timecourse experiment.

In Chapter 8 the relationship between perceived direction and heading error are tested within a clinical setting. In this chapter two case studies are described of patients with unilateral visual neglect. Three right-hemisphere control patients are also included. If an observer utilises the egocentric direction of a target to enable them to walk in a straight path towards it, then specific predictions can be made when egocentric direction is endogenously displaced, as is the case in visual neglect (e.g. Ferber & Karnath, 1999). It is found that a clinically related misperception of direction can have an effect on walking direction similar to that induced by prisms in healthy observers. In turn, the results show that prisms can also be used to alter the heading direction of patients in a similar manner to that found in healthy observers.

Chapter 2: Introducing an error in perceived egocentric direction and assessing the site and magnitude of adaptation.

The use of prisms

The most informative method for studying recalibration involves introducing some form of misalignment, or distortion, of a known amount and onset: if sensory input is disrupted in a quantifiable manner, then observing the behavioural output can enable inferences to be made with regards to the processes involved in recalibration. The most commonly used, and most productive, method for investigating recalibration in this way has been the use of wedge prisms. It was the early work of Held (e.g. Held & Hein, 1958; Held & Gottlieb, 1958) that sparked a re-interest into the use of prisms as a way of measuring perceptual-motor adaptation.

By looking through these optical devices, an observer experiences a quantifiable transformation of their visual world. Paired wedge prisms rotate vision relative to the observer, in turn displacing the apparent position of objects in the visual scene. Prisms mounted with their base to the left displace vision rightwards, whereas base right prisms displace vision to the left (see Figure 2.1). As a consequence of the induced misperception of direction, visually guided behaviour is notably disrupted: in general, movements towards objects are guided to the position in space where the object is perceived to be through the prisms.

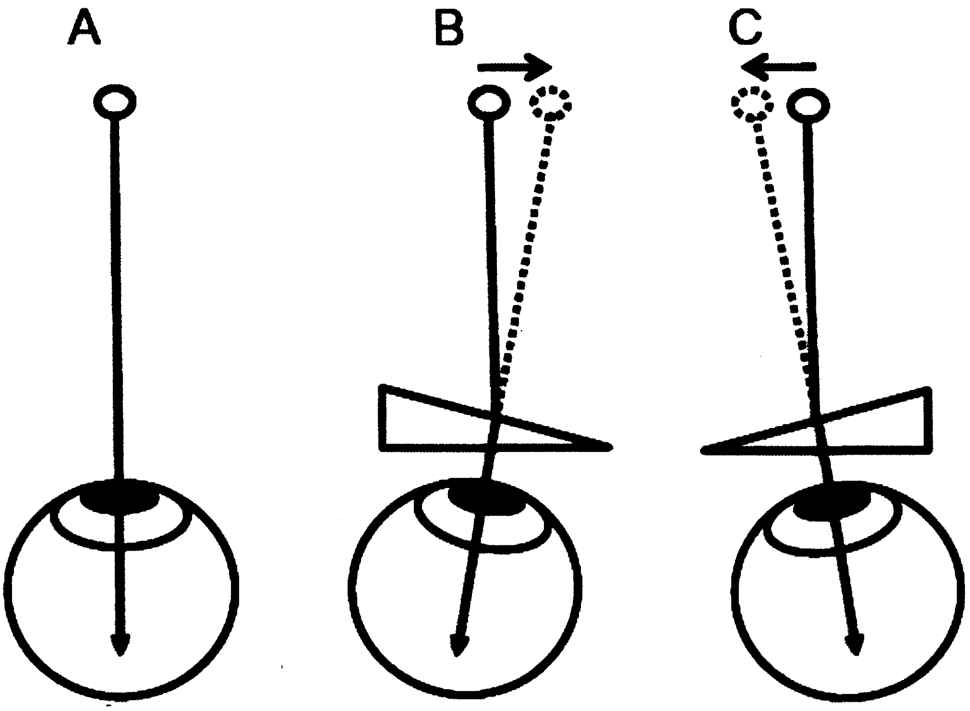

Figure 2.1. Schematic representation of (A) perceived target location in the absence of prisms; (B) perceived target location through base left, rightward displacing prisms; (C) perceived target location through base right, leftward displacing prisms.

Limitations

Prisms have been the tools of choice for investigating perceptual-motor recalibration for well over a century; however, they are not without their critics. Given that several authors have noted the potential for prisms to distort visual information, highlighting potential confounding artefacts related to the use of prisms is particularly important to the research presented here. For example, it has been argued that optical prisms may warp the normal flow field viewed by observers. With regards to the strategy used for the visual guidance of locomotion, it has been suggested that these distortions cause observers to rely on one source of visual information over another: namely, egocentric direction over optic flow (Warren, Kay, Zosh, Duchon & Sahuc, 2001).

Figure 2.2 (taken from Rock, 1966) illustrates how some scientists imagine how prisms may warp the visual array, by bending objects within it. However, contrast this illustration with the photographs shown in Figure 2.3.

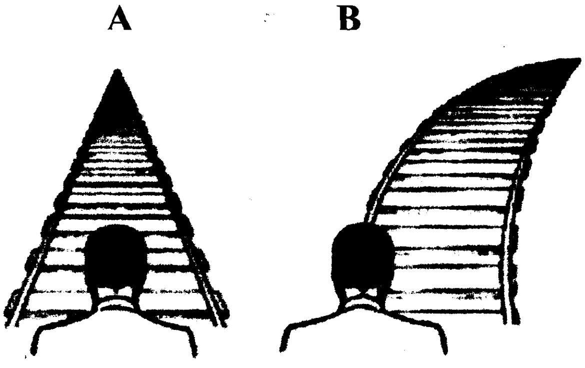

Figure 2.2. Representation of the suggested distortion viewed through prisms. A: the scene without prisms. B: the scene as perceived through prisms. Taken from Rock (1966, p107).

One of the images presented in Figure 2.3 was taken through the prisms used in the experiments presented in this thesis, and one was shot without the prisms. The distortion represented in Rock's illustration is not apparent. Indeed, it is very difficult to tell which one is which.

Figure 2.3. Both images show the experimental area used for all recalibration experiments presented throughout this thesis. The image on the left was taken through base right prisms that displaced the visual array 9° to the left. The image to the right was taken without prisms.

The prisms used in this thesis were custom designed, and it is clear from Figure 2.3 they were of high quality (see also Figure 2.12 for an image of the prisms) used. The minimal distortions caused by the prisms were thus unlikely to have had an effect on recalibration while walking.

Warren at al.'s (2001) assertion that prisms impair heading perception can be tested against empirical data. Several lines of research suggest that the perception of heading direction is tolerant to various distortions to the optic flow field: for example, Kim and Turvey (1998) found that when the flow field was distorted (e.g. using a spherical, or 'fishbowl' distortion) heading direction perception remained accurate. With regards to distortions caused specifically by prisms, Odom, Ghude and Humble (2006) examined the precision of observer's judgements of heading direction from optic flow fields in one of three conditions: wearing base left prisms, wearing base right prisms, or wearing no prisms at all. The precision of heading perception was found to be similar across all three conditions.

In light of this research, the choice of prisms to investigate the form of visual information used in recalibration remains a valid one: it is unlikely that the minor distortions will affect the optic flow field to such an extent that observers will be forced to use one source of visual information over another. The distortion objection of Warren and collaborators can thus be dismissed.

A further criticism related to the use of prisms is concerned with a different aspect of the flow field: Harris and Carre (2001) suggested that prism glasses impose restrictions on an observers field of view that, in turn, might deny access to relevant parts of an optic flow field such as foreground flow. Although this is a valid point – prisms used in earlier research did impose quite dramatic restrictions on an observer's field of view (e.g. Redding et al., 1985 used a field of view of only 20°) – the prisms used in this thesis offer the same field of view as regular spectacles. However, Harris and Carre (2001) found that increasing foreground flow by asking observers to look downwards while walking did not significantly affect heading error – observers continued to walk in the predicted direction according to the induced displacement of the prisms.

Alternatives to prisms

Although prisms have been the most common tools for inducing a misperception of direction for well over a century, there are several other methods that have been employed. For example, eye muscle vibration (e.g. Roll & Roll, 1987, Velay, Roll, Lennerstrand & Roll, 1994) has been shown to produce an illusory shift in perceived visual direction in the vertical plane. Neck muscle vibration has also been shown to produce a similar shift in horizontally perceived direction that can vary in magnitude depending on the amplitude of the tremor (Biguer, Donaldson, Hein & Jeannerod, 1988). However, the practical constraints associated with using vibration devices are much greater than those associated with the use of prisms. Furthermore, the effect of the vibration can vary substantially between observers. For example, Biguer et al. (1988) reported a difference in perceived direction as great as 8.5° between participants for a given vibration amplitude. Thus, it is more difficult to produce a quantifiable misperception of direction using these methods.

More recently, the advent of new technologies has allowed virtual environments to be presented on head mounted displays (HMDs). Indeed, Bruggeman used HMDs to induce a misperception of direction in his experiments (Bruggeman et al., 2007; Bruggeman & Warren, 2010). One advantage of HMDs over prisms is that they allow unprecedented control over the environment that is presented to an observer. However, they also come with several limitations. For example, although HMDs are becoming more sophisticated, and are now less cumbersome to wear, they still suffer from image problems such as low spatial resolution, low update rates, and reduced field of view (e.g. the HMDs used by Bruggeman et al. offer only a 60° horizontal FOV; also, see Wann, Rushton & Mon-Williams, 1995, for a discussion of problems with stereoscopic depth associated with the use of HMDs). Furthermore, in comparison to the real-world environments that can be explored using prism glasses, the environments used in experiments that utilise HMDs (e.g. the environment used by Bruggeman et al. 2007 – See Figure 2.4), often lack ecological validity.

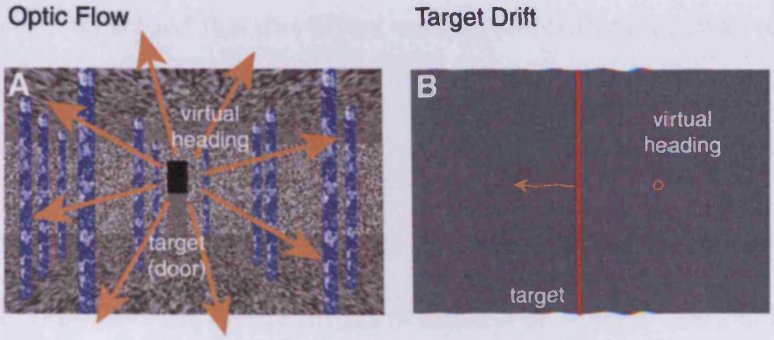

Figure 2.4. Experimental displays used by Bruggeman et al. (2007) in their adaptation experiment.

Thus, although several alternative methods of inducing a misperception of direction exist, the use of prisms is the most efficient.

The magnitude of perceived displacement viewed through prisms

Given that we have established that prisms are the best choice for introducing a misperception of direction, this section looks at factors associated with their use. Research conducted by Rock, Goldberg and Mack (1966) suggests that the structure of the optic array can exert an influence on the perception of visual direction through prisms. Rock et al. (1966) demonstrated that when wearing laterally displacing prism glasses in a dark room an observer's perception of a single luminous target is displaced precisely according to the power of the prisms. However, when the structure of the visual array was increased (by having observers view the same target, through the same pair of glasses, in a lit room), objects appeared to lie closer to their actual location. This result is now well known as the 'immediate correction effect' whereby a displaced image is perceived to be far less displaced than it actually is when viewing a structured scene. Redding and Wallace (2003) contended that observers rotating their shoulders when wearing the prisms could account for the effect. Harris (1974) argued that this effect is simply a result of an observer's interpretation of the term 'straight ahead'.

A finding reported by Rushton (2002) goes against the possibility that head-turns or a cognitive effect can account for the results of Rock et al. (1966). The findings of Rushton's (2002) experiment revealed that, as an observer moves further away from a target, the displacement perceived through the prisms becomes more in line with the power of the prisms. This distance effect suggests that a change in visual (retinal) information is responsible for the immediate correction reported by Rock et al. (1966).

Regardless of which explanation is correct, 'immediate correction' does appear to be a real effect. When first donning a pair of displacing prisms an observer will perceive the target to be to the left or right of its true location depending on the base of the prism. The magnitude of displacement is determined by the power of the prisms, and this can be attenuated by certain visual factors such as the structure of the visual array (Rock, Goldberg, & Mack, 1966) and distance from a target (Rushton, 2002).

The prisms used in this thesis displace (rotate) the visual array by 9°. However, given the research reviewed above, we conducted a short experiment to examine the magnitude of *perceived* displacement within the experimental environment used in our recalibration experiments. Observers (n=32) were required to stand at one of 12 positions that differed in distance from five surrounding targets. Once positioned, they were required carry out the following procedure: (i) close their eyes, (ii) put on the prisms, (iii) open their eyes, (iv) turn and face a target specified by the researcher, (v) close their eyes, and (vi) take two steps forward towards the target. This procedure was repeated at five different positions for each participant. Figure 2.5 shows the results of this experiment.

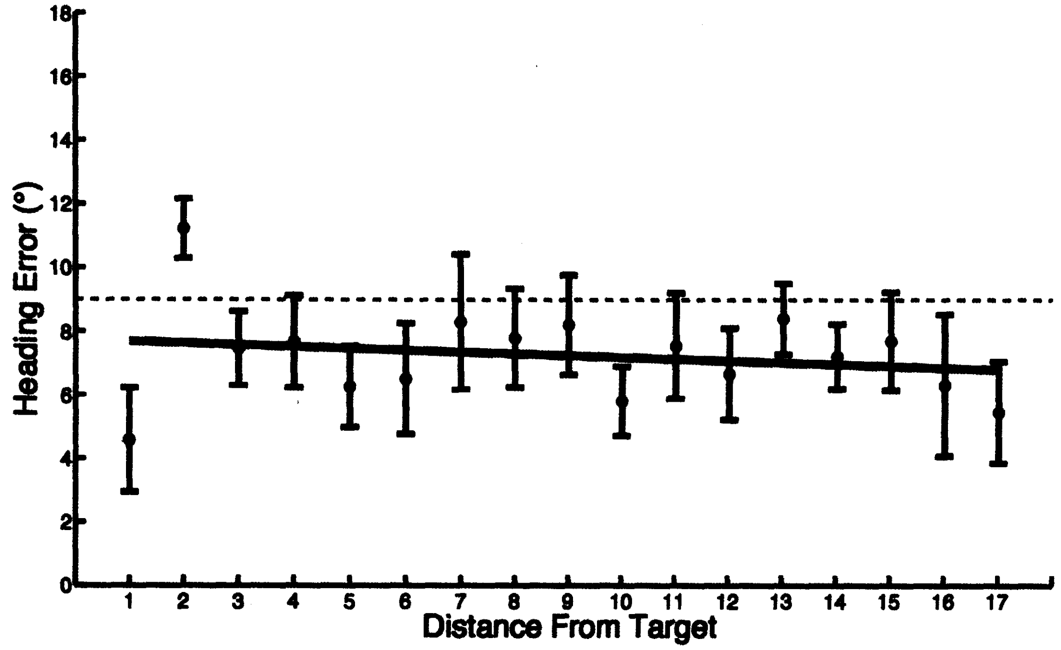

Figure 2.5. Mean heading error (perceived direction) as a function of distance from target. Dashed line indicates the displacement as defined by the power of the prisms. Error Bars = ± 1SE

The results presented in Figure 2.5 show that the displacement perceived through the prisms, in most cases, was less than the power of the prisms (indicated by the dashed line). Unlike the results of Rushton (2002) we were unable to find an effect of distance on perceived direction (see line fit), here the mean heading error hovered around 7°. We noted two perplexing outliers when observers were standing the closest to the target (i.e. at a distance of 1 and 2 metres), for which we have no explanation. However, apart from these two data points, the rest of the data indicates a constant effect, so we simply took a mean of the 17 distances form the target. Mean heading error across all distances was found to be 7.5° (SD = 0.39). The magnitude of perceived displacement was found to be significantly less than the actual displacement according to the power of the prisms [t (16) = -4.883, p < .001]. We use this 7.5° estimate in the experiments that follow to make more precise predictions with regards to the error in perceived direction induced by our prisms.

The sites of adaptation

Although it is clear that the error in perceived direction introduced by prisms is a visual one, recalibration can take place anywhere between the eyes and the feet (or hand) – the brain simply detects that an error has occurred somewhere within the perceptual-motor control loop. Possible forms of adaptation may include changes in registered retinal position, eye orientation, head orientation, limb position and movement direction. However, although multiple changes occur in various systems there is a considerable amount of evidence for changes in two key parts of the control loop (Hay & Pick, 1966; McLaughlin & Webster, 1967; Redding & Wallace, 1997): that responsible for the visual perception of the world (visual adaptation), and that responsible for the perception of felt limb position (proprioceptive adaptation).

The perceived visual direction of a viewed object is given by the eye-head system, and is comprised of retinal location, eye direction and head orientation. Proprioceptive or felt position of a touched object is given by arm-shoulder orientation, arm length, forearm-elbow orientation, forearm length, hand-wrist orientation, finger-hand orientation and the dimensions of the finger and palm – the hand-head system. Thus, although they can be mapped to a common reference frame (the trunk), and are linked for the purpose of visually guided action, visually specified direction and proprioceptively specified direction rely on different sensory signals (see Figure 2.6).

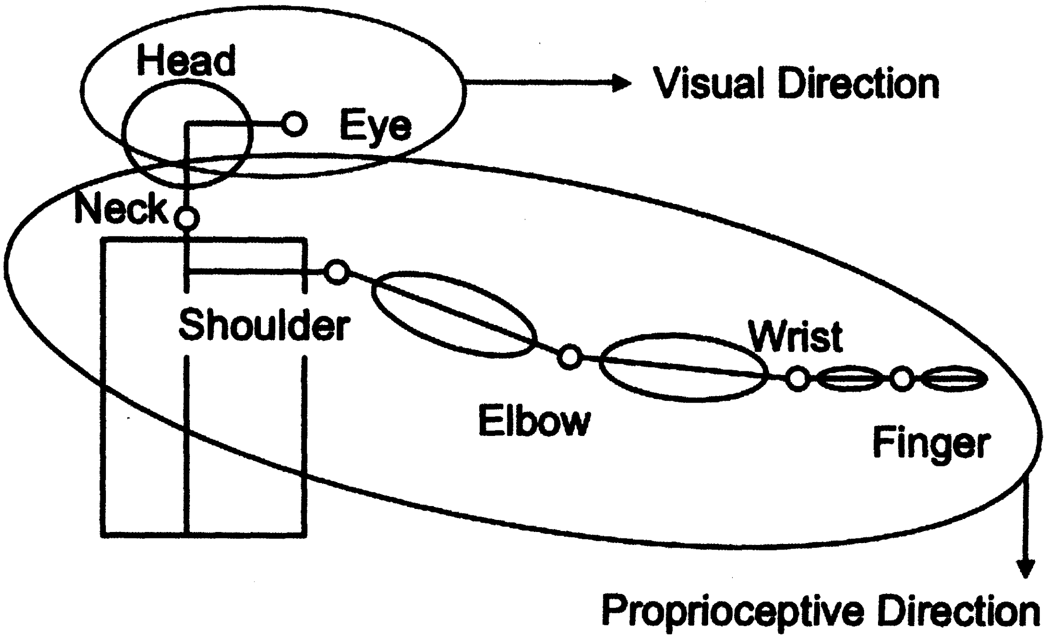

Figure 2.6. Illustration of the different sensory signals that are used to specify perceived direction. Visually specified direction is comprised of a change within the eye-head system (retinal location of the target, eye and head orientation). Proprioceptively specified direction is specified by a number of specific sub-systems: felt position of the head, shoulder, elbow, wrist, and finger. Adapted from Redding and Wallace (1992; 1997).

With regards to a change in visually perceived direction there was an early suggestion in the literature that this might be the result of a change in retinal location. Cohen (1966) found that if exposure to prisms was foveal then adaptation occurred only when effects were tested using foveal exposure; when prisms were presented 20° in the periphery, significantly less adaptation was found when the aftereffects were tested within the central part of vision. Cohen (1966) contended that these results provided evidence that adaptation had occurred in a specific retinal location. However, Crawshaw and Craske (1974) failed to replicate this finding, and contended that visual adaptation involves a change in registered eye position, and not retinal location. This suggestion is in line with current thinking – it is now generally agreed that the recalibration of visual direction does not represent a change in registered retinal position (e.g. Rock, 1975, Howard, 1982, although see Redding and Wallace, 2006).

Proprioceptive adaptation refers to a change in the position sense of body parts that lie outside of the visual (eye-head) system. Recalibration generally affects felt position from the hand to the head, including felt position of the head, shoulder, elbow, wrist and finger (Redding & Wallace, 1992). The measure used as an indication of proprioceptive recalibration (to be described below) is suggested to represent the sum of adaptation at these local sites within the hand-head system. Research by Wallace and Garret (1975) has provided evidence for additivity of recalibration within the local components of this system. Other changes can occur depending on the exposure conditions; for example, additivity of adaptation at local sites within the leg-hip system, including changes in hip, knee and ankle position, can also be found (e.g. Mikaelian, 1970). However, measures of proprioceptive adaptation are usually limited to changes in the hand-head system for two main reasons: (i) additivity within this system is particularly clear, and (ii) there is evidence to suggest that it can capture other forms of proprioceptive realignment after walking exposure (e.g. between the head and foot – Morton and Bastian (2004) revealed that adaptation while walking generalised to reaching, but not the other way around).

Changes within the visual and proprioceptive systems as a result of exposure to a visual displacement are thought to be complimentary and not opposing processes: both systems are thought to combine in a linear fashion to produce total adjustment in the perceptual motor control loop (Redding & Wallace, 1997). Thus, the sum of recalibration in local systems (visual and proprioceptive) should be equal to the sum of the total change in the whole control loop. Indeed, there are several lines of evidence to suggest that this is the case (e.g. Hay & Pick, 1966; Redding & Wallace, 1978; Redding & Wallace, 1993). The following section summarises how recalibration is measured.

Standard measures of recalibration

The general procedure for measuring recalibration involves assessing changes in task performance. Tasks are performed both prior to, and after exposure to, an optical displacement, without feedback, and under normal viewing conditions. Changes in task performance from pre- to post-exposure provide an aftereffect measure of prism adaptation. By using measures that are sensitive to detecting changes in particular systems, it is possible to isolate where within the perceptual motor control loop recalibration has taken place, while also providing an indication of the magnitude of recalibration.

As described in the previous chapter it was Held who set the standard for measuring recalibration using an exposure period with quantitative before and after measurements. The measure developed by Held and Gottlieb (1958) is presented in Figure 1.4 C. Several others later adopted Held and Gottlieb's technique to measure recalibration to a rearrangement of visual direction (e.g. Hamilton, 1964; Weinstein, Sersen & Weinstein, 1964; Hay & Pick, 1966; Efstathiou, 1969; Mikaelian, 1970; Moulden, 1971). However, the measure could not be used to isolate changes in specific sensorimotor systems since it involved both visual and proprioceptive components. Similarly, more recent methods of measuring recalibration by monitoring observer's walking direction once the rearrangement has been removed (Morton & Bastian, 2004; Bruggeman et al., 2007) suffer the same criticism.

Hay and Pick (1966) were one of the first to introduce specific tests to isolate changes in particular sensorimotor systems. The tasks included measuring changes in the ear-hand, ear-eye, ear-head, eye-hand, eye-head and head-hand systems. There were subtle differences between the tests to enable different forms of perceptual change to be measured. For example, recalibration in the ear-hand system was measured by asking a blindfolded participant to mark the position of an auditory target; however, the measure of ear-eye recalibration required sighted observers to identify the location of a concealed auditory target.

Hay and Pick (1966) found recalibration in each of the sensory systems measured (except for the ear-head system); however, some measures revealed almost identical magnitudes of adaptation (see Figure 2.7). For example, recalibration in the ear-eye and eye-head system was very similar, and so was the amount of adaptation obtained from the ear-hand and head-hand systems. It is suggested that the former two measures represent recalibration within the visual system, whereas the latter two represent changes in the proprioceptive system as described above. The remaining measure – eye-hand – was found to produce the greatest amount of adaptation. In fact, the amount of recalibration obtained was found to equal the sum of recalibration in the ear-eye and the ear-hand systems, suggesting that both systems are involved in the same process of eye-hand coordination. Interestingly, the eye-hand measure adopted the method of Held and Gottlieb (1958) and so involved both a visual and proprioceptive component.

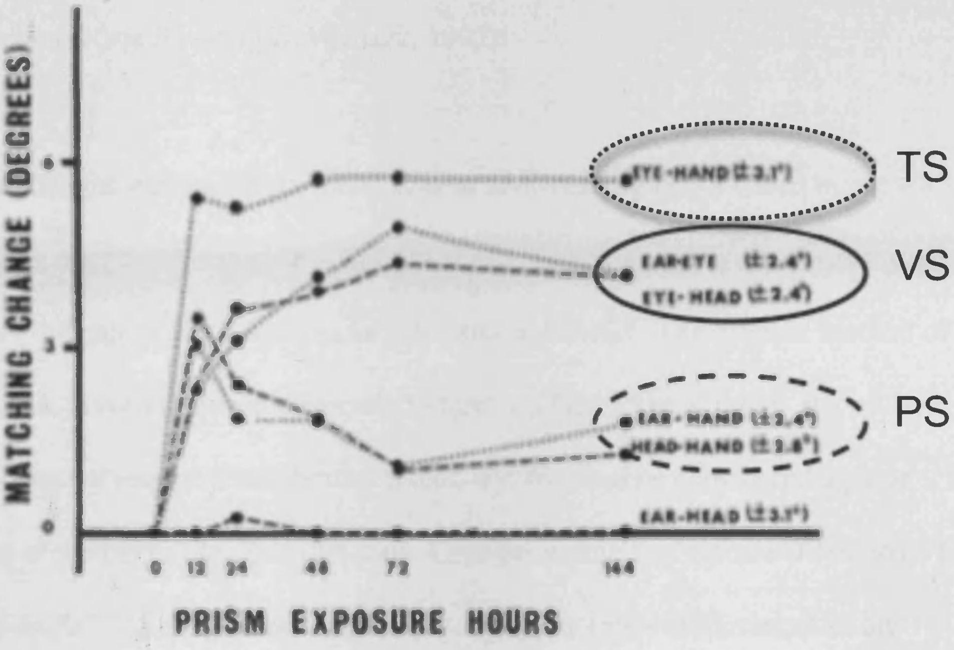

Figure 2.7. Data taken from Hay and Pick (1966). Note that the magnitude of Ear-Eye and Eye-Head recalibration is similar. The same also applied to the magnitude of adaptation found in the Ear-Hand and Hand-Head measures. The measures are thus thought to be tapping into the same perceptual motor system. Recalibration within the Eye-Hand system is always larger and was not significantly different from the sum of

recalibration within the visual (VS – visual shift) and proprioceptive (PS- proprioceptive) systems. This measure is thought to represent total recalibration within the entire perceptual-motor control loop (TS – total shift).

By using measures that provide an indication of overall adaptation within a particular system, researchers can dramatically reduce the number of tests that are used. This is particularly important given that recalibration is known to be short lived once the misperception of direction (i.e. prisms) has been removed (e.g. Choe & Welch, 1974). Based on the findings of Hay and Pick (1966) standardised tests of recalibration within the visual and proprioceptive systems, and also total recalibration, have now been developed (see Redding & Wallace, 1997).

A test for changes within the eye-head system involves aligning a visual target with a primary axis of egocentric space – straight ahead. To achieve this, observers are asked to verbally indicate when a moving target is straight ahead. The original method of Hay and Pick (1966) required observers to turn and face a visual target, the revised measure does not require a motor movement, and thus can be considered a purer indication of visually perceived direction. Changes within this system are referred to as 'visual shifts' (VS) or 'visual adaptation' since they reflect differences in the perceived visual location of straight ahead. However, as highlighted above, although a change is measured using a visual task this is not to say that an observer experiences a visual change: what is actually measured is a change in perceived eye or head orientation (or a change in proprioception/efference copy of the eye muscles as described by Howard, 1982). It may thus be more appropriate to refer to this change as a 'eye/head proprioceptive shift'; however, for simplicity, and to remain in line with the conventions of Redding and Wallace (1997), I will continue to use the term 'visual shift' to refer to a change in visually perceived straight ahead.

Changes within the proprioceptive system (proprioceptive shift, PS), or felt limb position, are also measured by asking the observer to indicate straight ahead. In this task, the observer is required to slowly guide their unseen arm to a position that they perceive to be straight ahead. This measure is similar to the combination of ear-hand and head-hand measures used by Hay and Pick (1966). Since visual input is absent in this task, any changes in the localisation of straight ahead are thought to reflect recalibrated proprioceptive input. A third aftereffect measure that is commonly used reflects total realignment within the perceptual motor system. To measure total adjustment (or total shift, TS) observers are required to point to a visual target without feedback of the position of their limb. This task thus involves coordination of both the visual and proprioceptive system.

Depending on the task that an observer is required to conduct while exposed to an optical rearrangement, the magnitude and location of recalibration can vary. For example, using a pointing paradigm, Redding and Wallace (1988) established that 'concurrent' exposure, whereby an observer views their arm as they guide it to a target, produced a greater amount of proprioceptive adaptation. In contrast, 'terminal' exposure, that only allows sight of the end-point of a pointing movement, was more conducive to visual adaptation. However, while walking, recalibration occurs within both perceptual-motor systems (e.g. Hay & Pick, 1966; Redding et al., 1985; Redding & Wallace, 1985a), perhaps because locomotion involves movement within multiple systems.

Note on the 'straight-ahead shift'

The primary motivation for using straight ahead rather than any other egocentric direction is that it falls on one of the primary axes of egocentric space. However, the use of straight-ahead as a fixed reference in space to measure recalibration has been criticised: Harris (1974) suggested that a change in perceived straight ahead may reflect a cognitive shift, and not a perceptual shift as assumed in the above measures. To avoid the possibility of obtaining misleading results, Harris (1974) contended that tests of recalibration should not include this internal reference point, and instead should follow the example of Templeton, Howard and Wilkinson (1974). In their experiment, Templeton et al. (1974) asked observers to point with their hand or eyes to a part of their own body, such as their big toe or resting hand, rather than pointing straight ahead. Similarly, Van Beers, Wolpert and Haggard (2002) and Simani, McGuire and Sabes (2007) asked observers to point to their own fingertip. However, although this method provides a measure of the realignment between proprioceptive and visual sensory modalities combined, it does not provide a pure measure of recalibrated egocentric direction. Furthermore, Redding & Wallace (1976; 2003) have rejected the idea that the cognitive effects related to perceived straight ahead significantly influence measures of recalibration. They suggest that the effect measured by Harris (1974) was the result of his exposure conditions inducing a change in felt head position. The use of perceived direction thus remains a valid way to measure recalibration, and is still the most common method.

Direction of adaptation

Visual and proprioceptive adaptation are additive to total recalibration and thus occur in the same direction (the direction of the prismatic displacement). However, changes in perceived straight ahead are expected to occur in quite specific and different directions. Below is a description of the directions of adaptation expected with a brief explanation of why this occurs (see Figure 2.8)

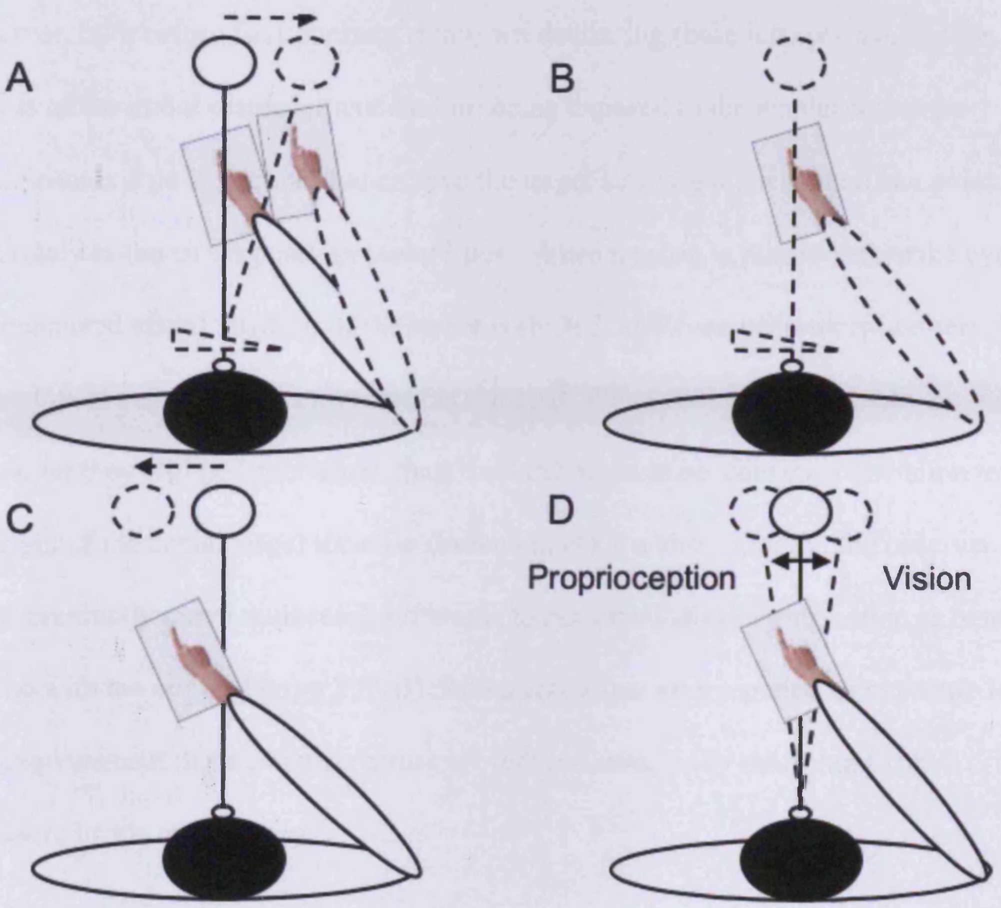

Figure 2.8. Illustration of a pointing paradigm to highlight adaptive directions of visual and proprioceptive shifts (Redding & Wallace, 1997). A: under normal viewing conditions an observer is able to accurately point to a target located straight ahead (solid lines); however, with the introduction of rightward displacing prisms, pointing

behaviour is duly affected (dashed lines). After a period of time the observer will adapt and pointing is again in line with the true target location (B). Once the prisms are removed, the observer will demonstrate a proprioceptive aftereffect to the left (C, D), in the opposite direction to the induced misperception of direction. However, perceived visual direction shifts to the right, in the same direction as the prismatic displacement (D).

Figure 2.8 (A) highlights the perceived position of a target placed straight ahead of an observer, both before first donning rightward displacing (base left) prisms, and the effects of the initial displacement. Before being exposed to the displacement the participant is able to accurately perceive the target as straight ahead, and can point accurately to the target position (solid lines). When a prism is placed before the eyes, the perceived visual position of the target is shifted; however, proprioception remains to the left of vision until a movement is initiated. When the observer initially points to the target they will point to where they 'see' the target to be, causing a deviation to the right of the actual target location (broken lines). To aim correctly, the observer must eventually move their reach leftwards to perceive their pointing action as being in line with the target. Figure 2.8 (B) demonstrates that after a period of exposure to the displacement these pointing errors are reduced, eventually returning to pre-exposure levels of accuracy.

Once the prisms have been removed (Figure 2.8, C), and the observer is asked to point straight ahead without feedback, the observer will initially point off to the left. Due to realignment while pointing, the hand feels to be to the left of it's true position, thus when asked to point straight ahead without vision, the observer will point to the left. The existence of such an aftereffect suggests that any corrections made while exposed to the displacement are not achieved by deliberately compensating for the distortion. If a change in pointing behaviour were achieved because of conscious correction, this would not be expected to continue once the observer is aware that the visual transformation has been removed (Harris, 1980).

With regards to visual adaptation using rightward displacing prisms (Figure 2.8, D), perceived visual direction is displaced to the right, causing the eyes (or head) to feel straight ahead when they are actually turned to the right. Thus, when participants are asked to position a visual target to be straight ahead of them, they will position it as being to the right. Producing aftereffects in opposite directions makes intuitive sense; any adaptive response must perceptually cancel out the discrepancy between vision and proprioception. Thus, if proprioceptive adaptation is drawn leftwards, visual adaptation is drawn rightwards. In this case, proprioceptive adaptation occurs in the direction opposite to the prismatic displacement, whereas visual adaptation shifts in the same direction as the displacement.

Although adaptation occurs in different directions for the two measures, when reporting adaptation results authors simply use the term ‘adaptive direction’, and flip the sign of one of their measures, assigning adaptation that occurred in the correct direction a positive value. Following on from the above description, after exposure to rightward prisms, both forms of realignments should combine to produce a shift in target pointing accuracy (total shift - TS). With regards to proprioceptive adaptation: if a target is positioned straight ahead of an observer, as a result of proprioceptive recalibration causing the arm to feel positioned to the left of its true location, a pointing error will occur to the left. Visual adaptation will add to this leftward shift: due to recalibration, visually perceived direction is shifted rightwards, as a result, a target that is positioned veridically straight ahead will be perceived to be to the left of straight ahead. Thus, when pointing to the perceived location of the visual target, the hand will be positioned leftward. The measure for total recalibration is therefore also suggested to produce a shift in the direction opposite to the prismatic displacement. Indeed TS is often reported to be larger than either component alone, and to not be significantly different to the sum of PS and VS (Redding & Wallace, 1997).

A further comment with regards to the measures used for adaptation concerns the fact that experimenters specifically requested that participants indicate straight ahead with reference to their nose. The reason for this request is uncertain; however, results from an unpublished experiment conducted by Redding (personal communication July, 2009) suggested that there are no differences between asking an observer to point straight ahead of their nose, compared to straight ahead of their trunk. This is surprising given that early work revealed that prism glasses could have quite profound effects on felt head position: for example, Kohler (1964) found that, towards the end of a prolonged period of exposure to prism glasses, observers came to rotate their head to one side while still perceiving it to be straight. However, since Redding and Wallace (1997) specifically indicate that they are interested in eye-head and hand-head systems, it makes sense to make estimates of straight ahead relative to some fixed position on the head (i.e. the nose).

With regards to the measures used in this thesis, estimates of perceived direction were made with reference to the trunk. Straight ahead was described to observers as being related to the mid-saggital plane of their body. Since Redding was unable to find a difference between estimates of straight ahead made relative to the head or trunk, this was not thought to be a significant factor in our experiments.

Our measures

The adaptation measures employed in this thesis were very similar to those developed and used by Redding and Wallace, described above. However, certain small changes were made to enable the measures to be recorded in an outdoor environment. Prior to, and after, exposure to the prisms participants were asked to complete three tasks to measure their level of adaptation. The tasks were completed without prisms. Differences in perceived straight-ahead from pre- to post-exposure (after-effects) were taken as an indication of an adaptive shift. For all tasks, measures were repeated four times, and participants stood 2 metres away from a wall. A ruler was attached to the wall to enable the experimenter to record the observer's indication of perceived straight ahead; the numbers on the ruler were small enough so that the participants were unable to recognise them. The setup for the measures of adaptation used throughout this thesis is illustrated in Figure 2.9.

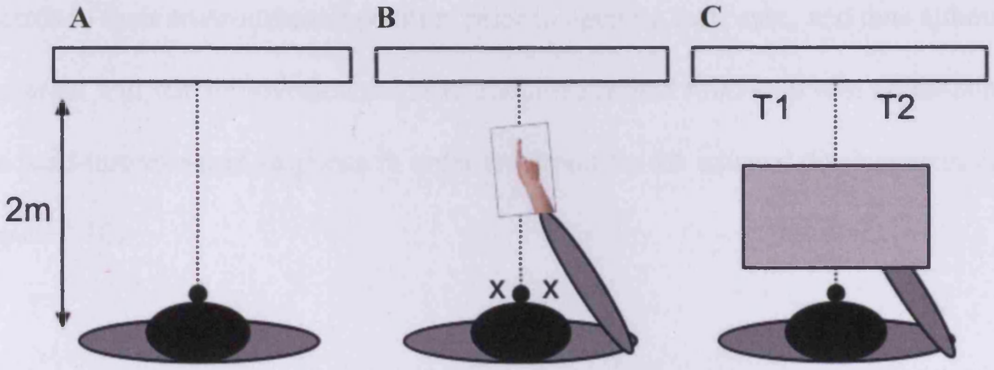

Figure 2.9. Illustration of adaptation measures. A: visual adaptation (Eye-Head system). B: proprioceptive adaptation (Hand-Head system). C: total adaptation (Eye-Hand system). T1 and T2 represent the two target positions for the total-shift task.

Visual changes (Figure 2.9 A) were measured by asking participants to verbally indicate when a visual target was straight ahead. The position of the observer was changed to prevent them from using a remembered position on the wall to make their estimates. Four positions relative to the wall were used – 15° and 30° to the left and right of the straight surface. The ordering of the angles was randomised such that observers sometimes began by facing rightwards, and other times began by facing leftwards. There was no movement involved in making this estimate, so any changes from pre- to post-exposure were assumed to represent changes in visually perceived direction. Although this measure does not allow us to distinguish whether changes occurred in the signalling of the position of the head relative to the shoulders, or of the eyes relative to the head, we included a technique to decrease the propensity to turn the head or eyes: before donning the prisms observers were required to close their eyes, they then put the glasses on, and were rotated two times before opening their eyes. In using this technique, observers did not have any expectations with regards to their environmental position prior to opening their eyes, and thus although the target will still be foveated the head and torso should follow, in turn eliminating the head-turn/eye-turn response in order to correct for the induced displacement (see Figure 2.10).

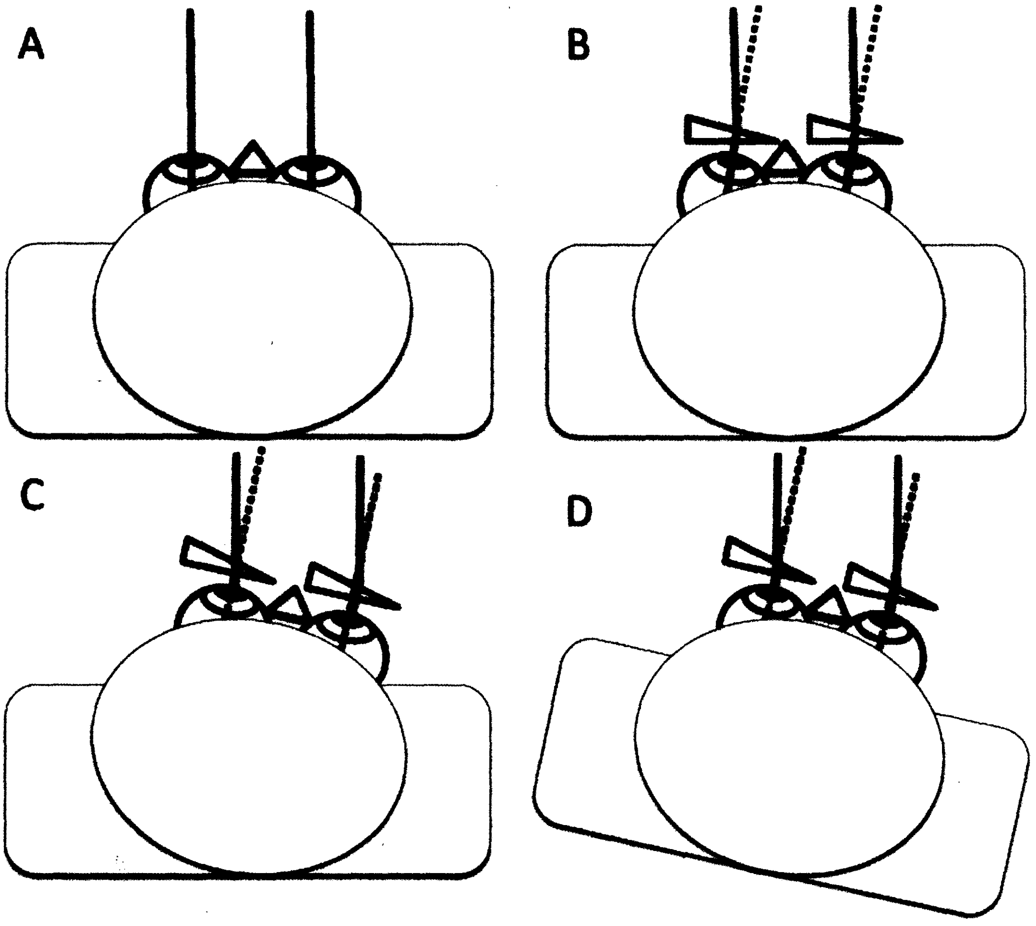

Figure 2.10. Schematic representation of head and eye posture when viewing a straight ahead target (A) without prisms; (B) through base left, rightward displacing prisms with a fixed head position (typical prism adaptation experiment); (C) through base left, rightward displacing prisms with a fixed body (typical prism adaptation experiment); (D) through base left, rightward displacing prisms with a non-fixed body (our experiment). Note in schematic D observers align their torso with the perceived target location, minimising any rotation in head or eye-posture. We anticipate that we

obtained D in our experiments since participants were asked to close their eyes before donning the prisms and were turned 1.5 times; in doing this participants did not have any prior expectations as to the locations of objects within the visual field, they should thus not attempt to compensate for the displacement by rotating their eyes and/or head.

Proprioceptive adaptation was measured by asking participants to stand parallel to the facing wall (Figure 2.9 B). With their eyes closed, participants were required to position their arm so that it felt that it was pointing straight ahead. When the observer was confident in their estimate, they were required to turn on a laser pointer, held in their pointing hand, to enable the experimenter to record their estimate of straight ahead. Since a visual stimulus is not present in this task, errors in localisation are believed to be the result of a change in recalibrated proprioceptive input. As previously discussed, change in the adaptive direction for either measure is assigned a positive value.

The test for total shift required participants to hold a piece of card (29 x 22 cm) under their nose with their left hand (Figure 2.9 C). This was a necessary measure to prevent participants from viewing their right arm as they were pointing; this would provide feedback to their pointing accuracy, and give them an opportunity to adjust their aim. Total shift was obtained by having the participant guide their unseen arm to one of two visual targets (circles of blue-tac approximately 2 cm in diameter) stuck to the wall. One target was located 15 cm to the left, and the other 15 cm to the right of true straight ahead; both were positioned 150 centimetres high (approximately eye level). When the participant felt confident that they were pointing towards the target, they were required to close their eyes, and turn on the laser pointer to enable the researcher to determine the accuracy of their estimate while preventing any feedback to the observer. Four measures were taken prior to and after exposure to prisms.

Why measure proprioceptive shift?

An often-asked question is: how can a pointing task reveal anything about proprioceptive recalibration while walking? When answering this question we can consider the findings of Morton and Bastian (2004). In their experiment (described in greater detail in the previous chapter) adaptation was found to generalise from a walking exposure task to a reaching exposure task, but not from a reaching task to a walking task. The results of this experiment thus highlight that a task involving an arm-movement can inform us about proprioceptive change after walking. With regards to why this should occur, Morton and Bastian made the following suggestions: (1) as a result of a change in the felt position of the head relative to the body; (2) a change in the translation from vision to action (i.e. the motor command); (3) as a result of a 'distributed proprioceptive shift' that occurred at multiple sites throughout the perceptual motor system (i.e. it is possible that shifts in the felt position of the eyes, head, and trunk – that are likely to occur during whole body movements – also generalise to limb movements). Although the authors were unable to distinguish between these possibilities, the point of relevance here is that an arm movement was able to pick-up proprioceptive changes while walking.

The measures adopted throughout this thesis are based on the accepted methods developed by Redding and Wallace (see Redding and Wallace, 1997) to directly test for visual and proprioceptive shifts. Indeed, in their own walking experiments

Redding and Wallace (e.g. Redding & Wallace, 1985b) were able to obtain substantial proprioceptive recalibration using a similar pointing procedure to that adopted here. Proprioceptive adaptation was also one of the primary sites of adaptation highlighted in Hay and Pick's (1966) seminal paper. We therefore believed it to be imperative to take both visual and proprioceptive measures in our experiments. However, as we reveal later in Chapter 6, although proprioceptive adaptation (as measured by an arm movement) does occur in the walking observer, the shift magnitude does not speak directly to the change in walking behaviour during the exposure period, and thus may not be as informative as we imagined. In Chapter 6 we make a few speculations as to why this might be the case.

Problems with the measure of total shift

Upon completing the first two rearrangement experiments to be reported in the next chapter (NoFlow and FOV), it became obvious that the measure for total shift was somehow confounded: over-additivity[3] for both experiments was found, whereby the sum of PS and VS alone was much greater than the aftereffect obtained using the measure for total recalibration (TS < PS + VS, see Figure 2.11 for an example). Since the adaptation measures were randomised to prevent adaptation decay affecting one particular task, the ordering of the pre- and post-exposure tasks cannot account for the general reduction in TS.

Instead, it is believed that the circumstances under which the TS measure was taken may have caused a decrease in the magnitude of TS reported. This is thought to be the

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[3] Could also be referred to as under-additivity since TS is always less than the combined sum of PS and VS. However, in line with the work of Redding and Wallace (1978), the term over-additivity is used here.

case for several reasons: (i) the cardboard that was used to conceal the observers arm, although was sufficient to do so, may not have occluded the moving limb if observers did not hold the board in the correct position (i.e. in a flat position parallel to the ground plane, directly under their nose); (ii) it was possible that if observers moved their arm up too high when making the pointing action, they may have been able to see the tip of the hand, which would have provided a cue as to their pointing accuracy; (iii) even if observers were unable to see their pointing arm, the hand with which they held the card was visible. It is thus possible that observers were able to make a relative movement by working out the position of the target relative to the seen hand; (iv) observers were positioned in front of the side of a building, the surface of which was somewhat reflective; it thus remains possible that observers were able to guide the reflection of their arm to the perceived target location. In this example proprioceptive adaptation would be under-represented in the measure since the arm would be visually and not proprioceptively guided, in turn, this would produce a reduced aftereffect. Finally (v) to enable the researcher to determine the accuracy of the pointing movement, while keeping knowledge of results concealed from the observer, when observers perceived that their felt arm position coincided with the visual target, they were required to close their eyes, and turn on the laser pointer. Although the experimenter closely monitored observer's eyes, it is still possible that observers were able to take a quick glimpse at their pointing accuracy, and adjust their arm position accordingly. This would also produce an aftereffect that is unrepresentative of total adaptation.

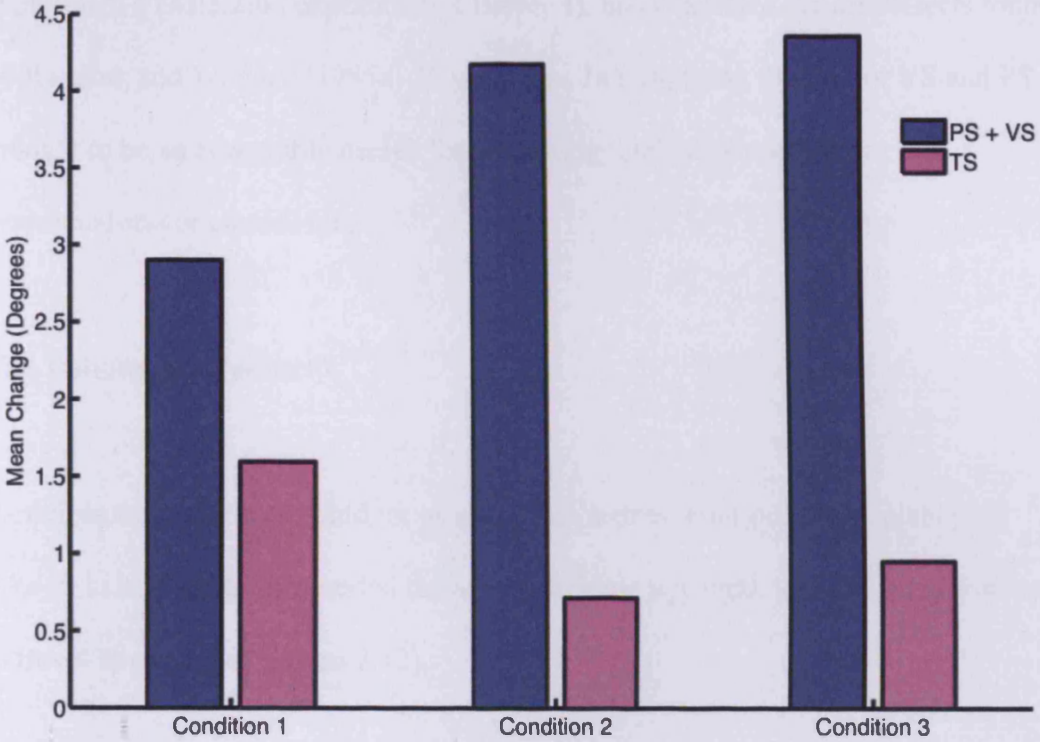

Figure 2.11. Illustration of the over-additivity (TS < PS + VS) found in the adaptation results. The results shown are of the aftereffects found for experiment 1 – the NoFlow experiment.

For the reasons outlined above, the TS measure is not reported in this thesis; any reference to total adaptation will concern the numeric sum of VS and PS measures. Since it has been specified that additivity within the perceptual motor control loop is the rule, and not the exception, and over additivity is rarely found (Redding & Wallace, 1997), the lack of a relationship between PS + VS and the measure of TS found in the initial few experiments is thought to be due to a combination of the problems highlighted above, and not due to some artefact of the exposure conditions or measures. Visual and proprioceptive adaptation are not thought to be influenced by any of these factors since they are not made in regard to some external reference within the environment. The lack of contamination in these measures is highlighted in the repeatability of the findings presented in Chapters 3, and also in the results of experiment 4 (Attention experiment, Chapter 4), that replicated the aftereffects found by Redding and Wallace (1985a) 25 years ago. In turn, using the sum of VS and PS is thought to be an acceptable means for presenting total adaptation within the perceptual-motor control loop.

The walking environment

Participants walked in an outdoor area of 17x5 metres. Four buildings, plant pots, bike racks and sheds surrounded the area, providing a natural, textured environment to travel through (see Figure 2.12).

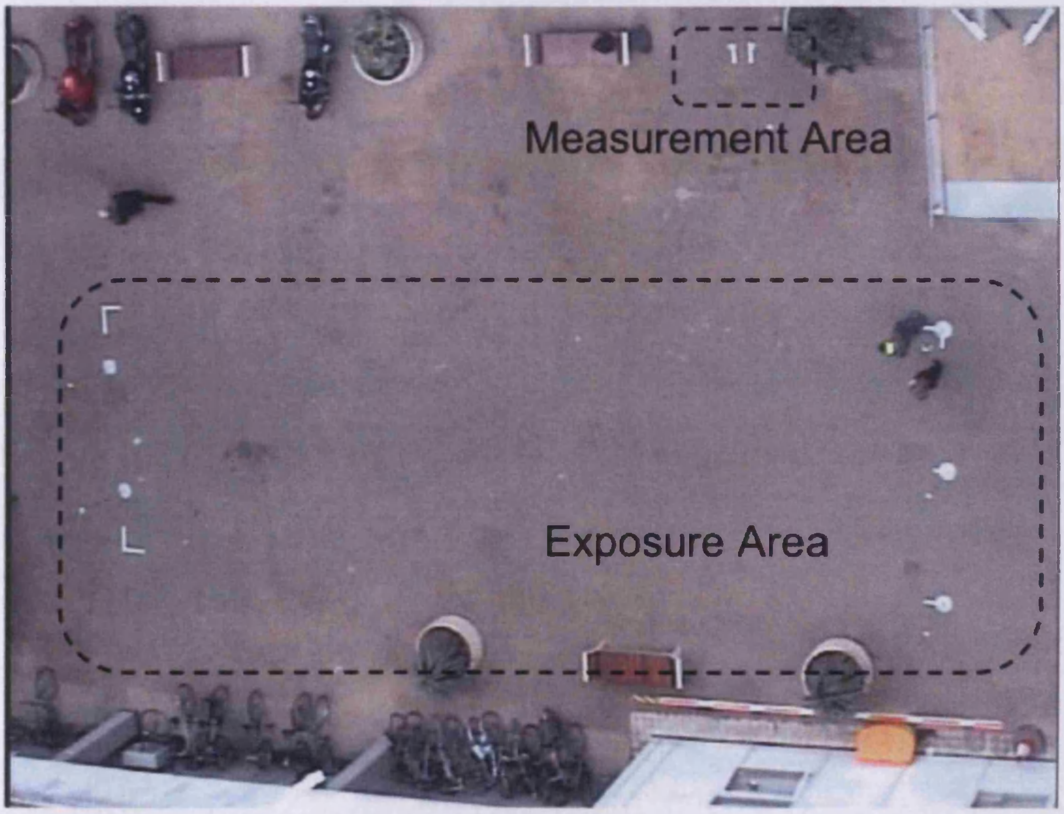

Figure 2.12. An image of the environment as recorded from the 12th floor balcony of the School of Psychology. As can be seen, luminous material was attached to the tips of the targets, and participants were required to wear a luminous hat, to aid

subsequent trajectory analysis (Chapters 6 and 7). Two strips of tape in the top-right of the image indicate the 'measurement area'.

The environments used in previous studies have varied substantially. For example, the environments used by Warren et al., (2001), and Redding and Wallace (1985a) were different to that used by Rushton et al. (1998). Rushton et al. used a natural open space, whereas Warren, and Redding and Wallace, used enclosed, man-made environments. The latter contain many more potential cues to heading direction (e.g. positional cues, described below) than the former.

Several lines of research highlight the possible effect of environment cues in heading perception. Research by Beusmans (1998) suggests that an individual's representation of the structural layout of an environment can affect heading direction, such that when the perceived structure of the environment was distorted, perception of heading was subsequently affected. Beusmans concluded that perspective changes could thus provide information about walking direction. Research by Hahn, Anderson and Saidpour (2003), found that observers could utilise information with regards to the change in perceived layout of the scene to give information about a change of viewpoint. The authors suggested that such information could be used for the online control of locomotion. Finally, research with rats has uncovered a wealth of evidence for the use of environmental cues to assist navigation; for example, the discovery of place cells (O'Keefe & Dostrovsky, 1971), head direction cells (Taube, Muller & Ranck, 1990), and grid cells (Hafting, Fyhn, Molden, Moser & Moser, 2005), have all highlighted the importance of positional information. Such positional information is not available in a large open field.

To ensure that our results were comparable, and not confounded by differences in the available cues, we used an enclosed space. The only cues we wished to minimise use of were alignment cues. To prevent observers from guiding their walking by aligning themselves with one of the straight walls within the environment, the following steps were taken: (i) only the corners of the area were marked out, and (ii) targets were positioned such that walking trajectories were diagonal in relation to the surrounding buildings. There were five targets, three located at one end of the rectangular area (one in each corner and one in the centre) and 2 at the other (located 1.5m in from each corner). A view of the environment at eye level can be seen in Figure 2.3; a plan view of the environment is shown in Figure 2.12.

General procedure

In all adaptation experiments participants wore a pair of displacing wedge prisms (horizontal field of view 110°), mounted in a set of thin-rimmed binocular spectacle frames (see Figure 2.13). Although individual observers were only exposed to one direction of displacement, two pairs of glasses were incorporated in all rearrangement experiments. One pair displaced the visual world an angle of 9° to the right, and the other by 9° to the left.

Figure 2.13. Base right, leftward displacing prisms.

The trial started by asking participants to close their eyes before donning the prisms. They were then rotated 1.5 times so that they were facing in the general direction of the target to which they were to walk towards (located at the other end of the rectangular area, at a distance of 17m). This initial routine was conducted for all participants, in all conditions, and was used to (i) prevent participants from seeing a shift in perceived direction, as they would if they stood still, and (ii) prevent participants from correcting for the displacement by simply turning their head or eyes to match the direction they were facing prior to putting the prisms on. Following this, the participant was instructed to open their eyes, and walk directly towards the target, specified randomly by the researcher as either the target on the left, the target on the right, or the target in the centre. This counted as one walking trajectory, the participant would then be instructed to turn and face the targets at the other end of the area, and again, walked to the target specified by the researcher.

Measures of adaptation were taken before and after exposure to the prisms in a 'measure' region off to the side of the 'exposure' area (approximately 5 metres away – see Figure 2.12). After the exposure period, observers were asked to close their eyes and were guided back to the measurement area by the experimenter who placed their feet in the correct positions ready to take the post-exposure measures. The participant was asked to close their eyes when travelling from the exposure area to the measurement area. This was to ensure that the magnitude of recalibration obtained was a function of walking between targets, and not a result of walking to the measurement area. It should be noted that there is the possibility that observers peeked while being guided. However, we believe that this would not have had a significant impact on the trends in our results, since 'peeking' would have been randomly distributed across groups. Furthermore, monitoring the behaviour of the observers, as they were being guided, suggests that peeking did not occur, or was minimal.

Chapter 3: Recalibration of Egocentric Space

When an error is introduced into the mapping between visual direction and the movement of the feet, an observer will initially take a curved path when walking to a stationary visual target (Rushton et al., 1998). After a period of walking, adaptation will occur, resulting in a straighter walking trajectory (Rogers & Spencer, 2005; Bruggeman et al., 2007). As explained in the introductory chapter, Held and Freedman (1963) suggested that visual motion due to self-movement (optic flow) could be used to recalibrate a misperception of direction while walking. A simple way to think of this is in terms of the focus of expansion of the flow field: when an observer (with fixed eyes and head) takes a step forward towards a target object he/she anticipates the FoE to be at the centre of their visual field. If the FoE is not where it is expected, an error signal (the discrepancy between the anticipated and experienced pattern of visual motion) is generated that drives recalibration (see Figure 1.5, Chapter 1).

As previously noted, most research has found both proprioceptive and visual adaptation while walking with a misperception of direction. However, a recent study by Bruggeman et al. (2007) reported that their data gives no indication of adaptation of perceived direction. They concluded that optic flow is not involved in the recalibration of straight ahead. This is a perplexing finding, and, if correct, very important. Therefore, using different methods, I revisited the issue in three experiments: in experiment 1, I temporally manipulated the availability of optic flow. In experiment 2, the availability of optic flow was manipulated spatially by restricting observer's field of view, and in experiment 3, the role of an error signal was examined.

Experiment 1: Exposure to displaced optic flow results in adaptation of visual straight ahead

In the first experiment the availability of optic flow while walking was manipulated temporally. While wearing prisms, participants walked toward a target while exposed to full, intermittent, or no optic flow. Perceived proprioceptive and visual straight ahead were measured before the experiment began, and then again after each exposure period. If straight ahead is recalibrated while walking, we should expect to find a change in perceived direction. If optic flow has a particular role (as suggested by Held and Freedman, 1963), then the change from pre- to post-exposure measures should be the largest when optic flow is continually available, and lowest when it is not available. If other factors are responsible for recalibration, the availability of optic flow should not have an effect, and a change in perceived direction should not differ between conditions.

Participants

A total of twenty-two participants took part in the study. Two were unable to complete all three experimental conditions due to a sudden change in the weather, and so were removed from the data analysis. All were right-handed undergraduate students from Cardiff University who received payment for their participation. All had normal or corrected to normal vision by contact lenses.

Procedure

To test for the involvement of optic flow in recalibration while walking, exposure to optic flow was manipulated in three conditions (see Figure 3.1): Flow, StopGo and NoFlow – that is, while walking, optic flow was available continuously, intermittently, or not at all. The order of the conditions was randomised across participants.

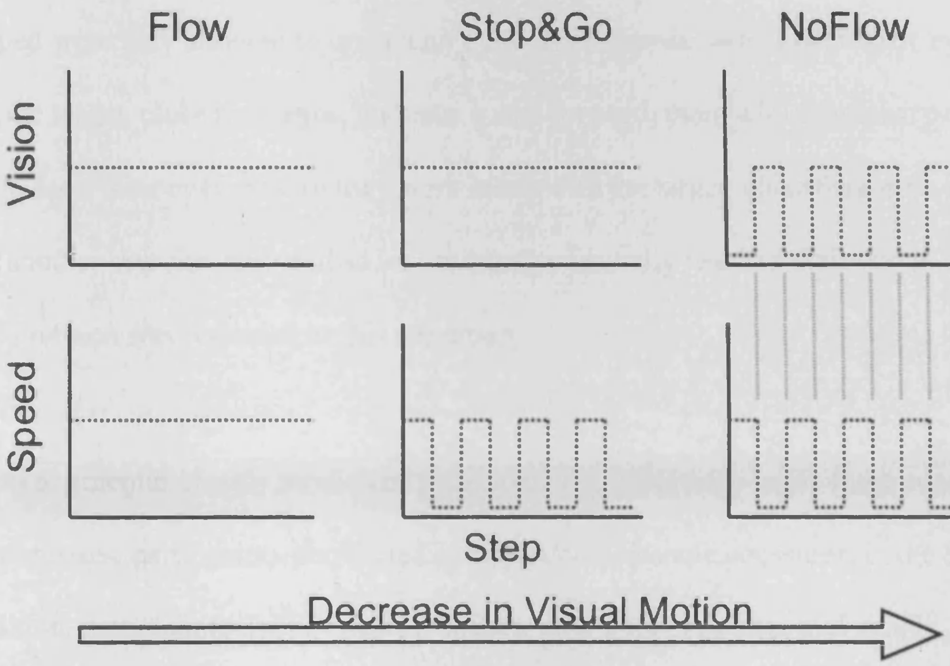

Figure 3.1. Schematic representation of the three experimental conditions. In the flow condition both speed of stepping and vision are continuous, whereas only vision is continuous in the StopGo condition (participants had to make a definite stop after every step). In the NoFlow condition both the speed of stepping and vision are discontinuous, such that when a step is made, vision is absent, when stepping has ceased, vision is present.

In the Flow condition participants were required to wear prism glasses and walk directly towards a target as they would under normal circumstances, thus visual motion was continuous throughout the trial. In the StopGo condition vision was continuous, but translation was not: participants were required to make a definite stop, bringing both feet together, for at least one second after each step. This condition created intermittent optic flow: participants did not receive the same build up of visual motion as they would in the 'Flow' condition. In a third condition – the NoFlow condition – both vision and locomotion were discontinuous and out of phase: participants had to make a definite stop after each step, and only when they were stopped were they allowed to open their eyes. The observer would open their eyes, face the target, close their eyes, and take a step forward, then, while stationary they would open their eyes, ensure they were inline with the target, close their eyes and take another step forward, and so on until they eventually reached their target. Thus, visual motion was removed in this condition.

The experimenter closely monitored participants' performance in the three conditions. In most cases, participants performed as requested. On some occasions, in the StopGo condition, participants did not make a definite stop after each step, and simply brushed their feet while walking. However, this was quickly rectified by a verbal request from the experimenter. Although it is possible that participants did experience some optic flow in the NoFlow condition, perhaps by mistakenly opening their eyes while moving, this is believed to be minimal. Due to the nature of the three different exposure tasks, the duration of exposure to the prisms was different in each condition, particularly in the StopGo condition, where exposure to the prisms was longest. However, this difference was only in the region of approximately one minute, and based on the results, was unlikely to have affected the trends in the data.

All participants took part in all three conditions with only the orientation of the prisms (either leftwards or rightwards) varying between participants. The ordering of direction exposure was random. Ten participants were exposed to base right prisms that displaced the visual array 9° leftwards, and ten participants wore base left prisms that laterally displaced their field of view 9° rightwards. There were six trajectories in each condition.

Participants were required to complete the three tasks that measured perceived direction prior to exposure to the first experimental condition, and then after each exposure session. Recalibration was inferred by comparing performance on the tasks from pre-to post-exposure (see Chapter 2 for details). The order in which the participants were required to complete the tasks was randomised across participants. Finally, after each condition, participants were given three minutes to de-adapt to the previous exposure. During this time participants were asked to walk around the outside of the 'exposure' environment while bouncing and catching a tennis ball. This task was used to accelerate de-adaptation since it provided ample feedback of various kinds with regards to the changed relationship between visual and proprioceptive systems. The method included five steps: (1) measures of straight ahead (pre); (2) exposure condition; (3) measures of straight ahead (post); (4) de-adapt to baseline; (5) repeat 2-4 for conditions 2 and 3.

In line with Held and Freedman's (1963) suggestion that optic flow is a prime source of reafferent visual information for recalibration, we predicted that the magnitude of *visual* recalibration would be greatest in the condition containing the most optic flow: the Flow condition. If optic flow does play an important role in recalibration, the change in perceived visual direction in the Flow condition should be significantly greater than recalibration in the NoFlow condition, when optic flow is absent. In his walking experiments Held (e.g. Held and Bossom, 1961; Held & Mikaelian, 1964) only measured changes in perceived visual direction. We were thus unable to make any precise predictions with regards to the effect of optic flow on proprioceptive recalibration.

Results and discussion

Mean estimates of visual and proprioceptive straight ahead prior to, and after each exposure phase are shown in Figure 3.2. Data for left and right prisms were combined.

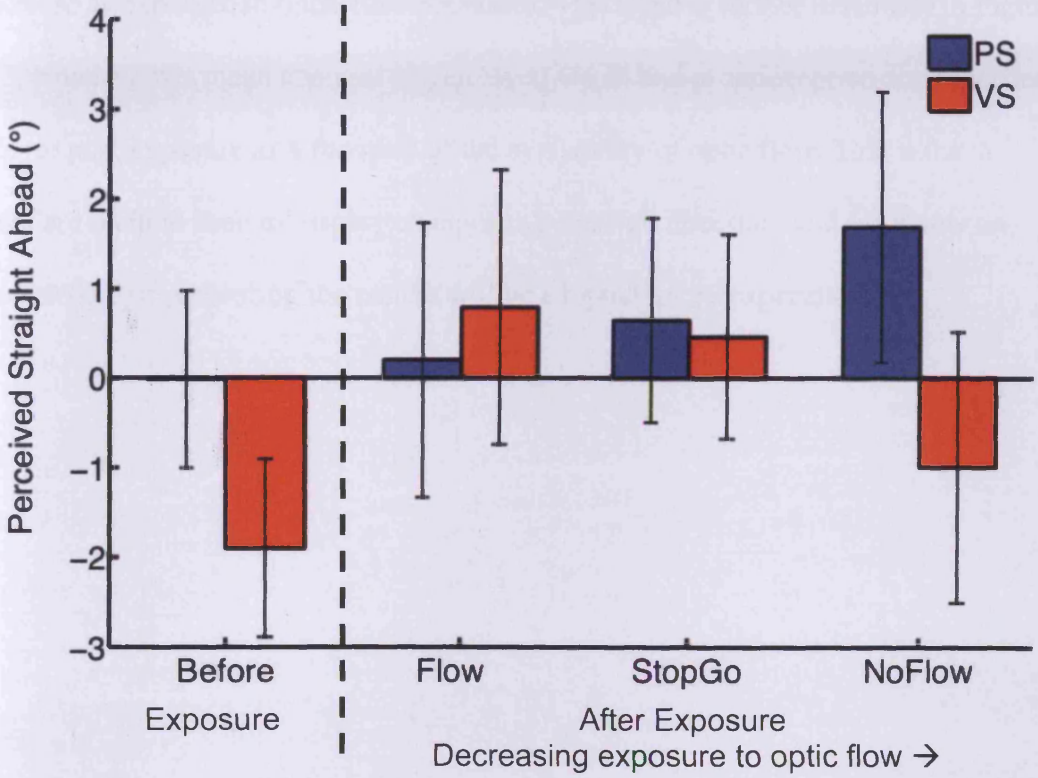

Figure 3.2. Mean estimates of straight ahead, before exposure to the prisms and then after each exposure condition. Negative values represent a deviation to the left of true

straight ahead (0°); positive values represent a deviation to the right of true straight ahead. Error Bars = ± - *SE.*

Interestingly, Figure 3.2 shows an inherent bias in perceived visual direction to the left of true straight ahead. It is well known that healthy participants exhibit a small leftward bias, a phenomenon known as pseudo-neglect (Bowers & Heilman, 1980). However, proprioceptive straight ahead is relatively accurate prior to exposure to the prisms. With regards to a change in perceived direction after prism exposure, there is a large shift in perceived visual straight ahead after exposure to prisms in the Flow condition, an effect that decreases as exposure to optic flow decreases. In contrast, there is little change in proprioceptive straight ahead from pre- to post-exposure in the Flow condition. Unlike visual recalibration, proprioceptive recalibration appears to increase as exposure to optic flow decreases. This trend is further illustrated in Figure 3.3, which shows mean changes in perceived visual and proprioceptive direction from pre- to post-exposure as a function of the availability of optic flow. This is the standard method used to display changes in perceived direction, and from now on, this method of presenting the results will be adopted for all experiments.

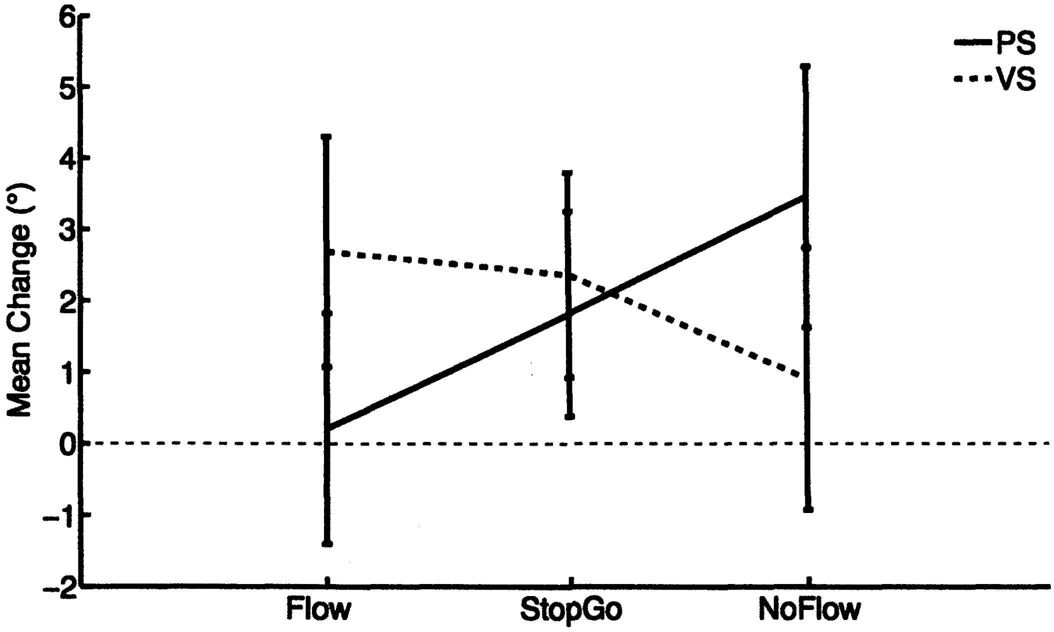

Figure 3.3. Mean adaptive shift for a left and right optical displacements combined. Level of visual shift (VS) and, proprioceptive shift (PS) are displayed as a function of the availability of optic flow. Error bars = ± 1SE (within subjects). Within subjects error was calculated taking the mean PS – mean VS for each individual participant, and was used to give a more accurate representation of the variability (Cumming & Finch, 2005).

Visual inspection of Figure 3.3 reveals that walking with continuous visual motion was sufficient to produce adaptation of visual straight ahead, but not proprioceptive straight ahead. As the availability of optic flow was reduced, so was the amount of visual adaptation. In turn, as exposure to optic flow decreased, proprioceptive adaptation increased. Visual and proprioceptive adaptation were found to be at a similar level in the StopGo condition where optic flow was available only intermittently.

Mauchly's test of sphericity was non-significant (p = .139), indicating that variances were equal, and validating the use of parametric statistics. From this point on, in proceeding statistical analyses, unless otherwise stated, it should be assumed that the data meets the assumption of sphericity.

Based on the a priori predictions we used one-tailed t-tests to examine if the magnitude of visual recalibration in the Flow condition was significantly greater than that in the NoFlow condition. The results were as predicted [t (19) = 1.668, p = .056], although only marginally so. The availability of continuous vs. intermittent flow did not significantly affect the amount of visual adaptation obtained (p = .38); however, the difference between StopGo and NoFlow did approach significance (p = .083). These findings lend support to the hypothesis that optic flow plays an important role in the recalibration of visually perceived direction, and hint at the possibility that exposure to intermittent flow is perhaps enough to produce recalibration.

With regards to a change in proprioceptive straight ahead, a difference was also found between the magnitude of proprioceptive adaptation in the Flow and NoFlow conditions; however, this was found to be in the opposite direction to that found for visual adaptation. Using a two-tailed t-test (we did not have a specific prediction with regards to the effect of optic flow on PS) we found that proprioceptive recalibration was significantly greater when optic flow was absent compared to when optic flow exposure was continuous [t (19) = -2.238, p = .037]. Similar to the analysis of visual adaptation, the change from Flow to StopGo was non-significant (p = .162). The difference between StopGo and NoFlow was also non-significant, although it did approach levels of significance (p = .077). Thus, in contrast to what was reported for visual recalibration, it appears that optic flow is not necessary to produce a change in proprioceptive straight ahead; indeed, proprioceptive adaptation is actually greater when optic flow is not present.

The results of experiment 1 provide clear evidence to suggest that misperceived egocentric direction is recalibrated within both the visual and proprioceptive systems. The site of adaptation is dependent upon the amount of optic flow available to the observer, with more optic flow resulting in more visual adaptation. However, the finding that proprioceptive adaptation occurred in the absence of optic flow suggests that some process other than the detection of discrepant visual motion enabled recalibration.

Although observers were only exposed to static visual information with regards to the position of the target after every step, it is still possible that intermittent target drift, from a change in direction, could account for this finding. It is also possible that the adaptation could be driven by discrepant positional information, such that observers anticipated where each step would position them in relation to objects within the environment (e.g. Beusmans, 1998; Andersen et al., 2003). The findings cast doubt upon the contention of Bruggeman et al. (2007) that optic flow is not involved in the recalibration of visual direction.

To investigate further the role of optic flow in the recalibration of egocentric direction, experiment 2 used a different technique; instead of temporally manipulating exposure to the optic flow field as done in experiment 1, experiment 2 manipulated optic flow by imposing a spatial restriction on participant's field of view.

Experiment 2: Visual adaptation requires a full field of view

Experiment 2 investigated the role of a restricted FOV on the magnitude and location of recalibration. Observers were exposed to optic flow while walking with either a full FOV or a restricted FOV. The availability of shutter goggles enabled the inclusion of a third condition. In this additional condition a further temporal manipulation was introduced to see if this added to the effect of a restricted FOV.

Participants

A total of thirty participants took part in the study. All were right-handed undergraduate students from Cardiff University who received payment for their participation. All had normal or corrected to normal vision by contact lenses.

Procedure

Three viewing conditions were evaluated (see Figure 3.4): two with a restricted FOV ('FOV' and 'Shutters') and one without in which participants were required to simply wear the prism glasses that afforded a field of view of 110° (a replication of the 'Flow' condition, experiment 1). Welding goggles from which the lenses were removed were used to restrict the FOV in the two conditions. Both conditions provided a restricted FOV of 80° horizontally. In one condition, participants simply wore the goggles over the prism glasses while walking (reduced FOV). In a second condition, an additional temporal manipulation (shutters) was introduced that involved temporally limiting the participant's exposure to the environment. This additional manipulation was included to determine whether the temporal influence revealed in experiment 1 would affect adaptation in an additive way when combined with a reduction in the spatial availability of optic flow (reduced FOV). To achieve this participants wore welding goggles that had a white opaque screen attached to the front. The screen was timed to give 400ms snapshots of the environment at 400ms intervals.

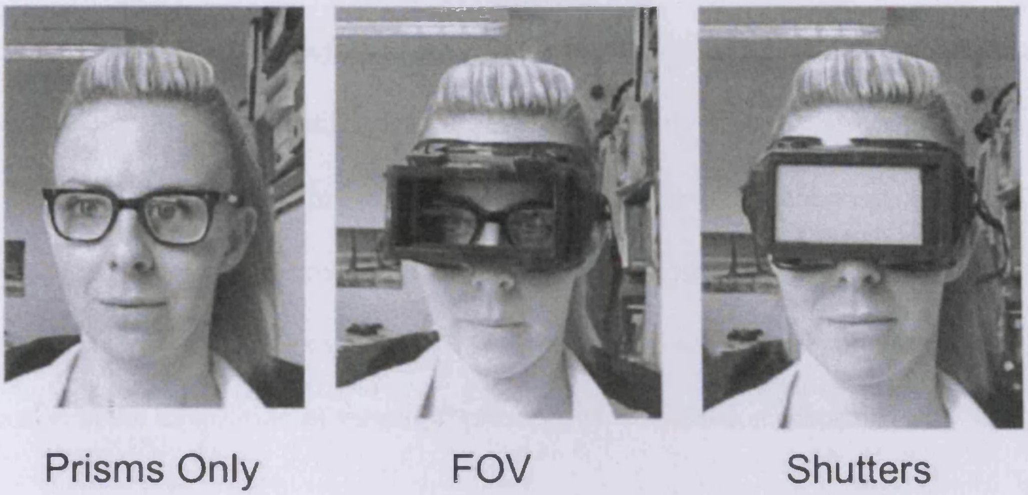

Figure 3.4. Illustration of the equipment worn by participants in the three conditions. The 'Prisms Only' condition is comparable to the Flow condition of experiment 1. The prisms shown in the 'Prisms Only' image were worn in all three conditions. Although this cannot be seen in the 'Shutters' image the glasses were worn underneath the goggles. The FOV was restricted to 80° horizontally in the 'FOV' and 'Shutters' conditions. The Shutters were made from electronic 'privacy glasses' which were set to give 400ms snapshots of the environment at 400ms intervals.

As in the previous experiment participants were required to walk back and forth between targets three times resulting in a total of six trajectories. Measures of perceived straight ahead were taken before the commencement of the first experimental trial, and after each exposure phase. After each condition there was a period of three minutes during which participants were required to walk about the ‘exposure’ area while bouncing and catching a tennis ball. This was to encourage de-adaptation before proceeding to the next condition. The order in which the participants were required to complete the experimental conditions and adaptation tasks was randomised across participants.

Based on the results of experiment 1 it was predicted that, if restricting an observer’s FOV to 80° is a sufficient infringement on the availability of optic flow, we should find a significant decrease in the magnitude of visual adaptation obtained, and an increase in proprioceptive recalibration. If the temporal manipulation was sufficient in reducing exposure to flow even further, then we should see a further decrease or increase in the magnitude of visual/proprioceptive recalibration accordingly.

Results and discussion

Adaptation for left and right prisms was combined, and adaptation in the correct (adaptive) direction was assigned a positive value (see Figure 3.5). The comparable results of experiment 1 are also displayed on the figure for comparison.

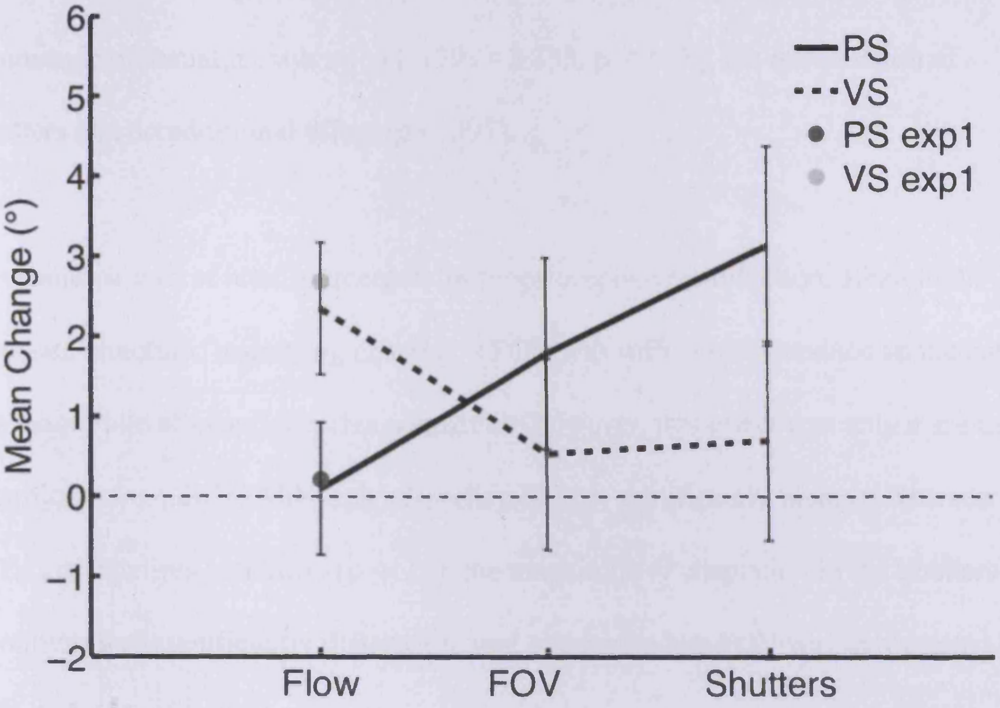

Figure 3.5. Mean adaptive shift for visual (VS) and proprioceptive (PS) adaptation as a function of restricted exposure to the optic flow field. Error bars = ± 1SE (within subjects).

The results reveal a decrease in visual adaptation and an increase in proprioceptive adaptation when exposure to optic flow is restricted. The temporal manipulation (Shutters) had a further influence on proprioceptive adaptation producing the greatest amount of proprioceptive recalibration across the three conditions. However, the introduction of the shutter goggles did not have a further influence on visual recalibration over that obtained with a restricted FOV. The magnitude of visual and proprioceptive recalibration in the comparable condition in experiment 1 map onto the results of this experiment quite nicely.

Similar to the analysis conducted for experiment 1, a series of one-tailed t-tests were used to examine our predictions. Analysis of the magnitude of visual recalibration revealed that reducing an observer's FOV was enough to significantly decrease the magnitude of visual recalibration [t (29) = 2.335, p = .013]; the introduction of shutters had no additional effect (p = .397).

A similar pattern of results emerged for proprioceptive recalibration, albeit in the opposite direction: restricting observer's FOV was sufficient to produce an increase in the magnitude of proprioceptive adaptation; however, this effect was only marginally significant (p = .067). Although adaptation did not significantly increase between the FOV and Shutters condition (p = .15), the magnitude of adaptation in the Shutters condition was significantly different to that obtained when FOV was unrestricted [t (29) = -2.553, p = .008].

These results are in line with those of experiment 1 showing that the availability of optic flow can have an important influence on the location of recalibration within the perceptual motor system. Similar to the temporal manipulation, changing the spatial properties of the optic flow field by decreasing an observer's FOV reduced the magnitude of visual recalibration, while increasing proprioceptive recalibration. We were unable to find evidence to suggest that combining spatial and temporal manipulations has an additive effect on adaptation magnitude, particularly in relation to visual adaptation that was effectively reduced to zero with the FOV restriction alone. However, although non-significant (p = .3), there is a trend in the data to suggest that introducing the shutters (temporal manipulation) had an additive effect on proprioceptive adaptation.

As an aside, the results of this study may be of some consequence for the locomotion studies that have used head mounted displays (HMDs). Typically, HMDs have rather restricted FOVs. For example, studies conducted within the Warren lab (e.g. Warren et al., 2001; Bruggeman et al., 2007) restrict the FOV to 60° in the horizontal dimension. This restriction is even greater than that imposed in our experiment. Bruggeman's (Bruggeman et al., 2007; Bruggeman & Warren, 2010) reported findings, which went against previously reported results, may be in line with the restricted FOV data reported here. However, it is not possible to make a direct comparison because Bruggeman et al. did not use the same measures of perceived straight ahead, and the measure that they did use was problematic.

Research conducted by Guterman, Allison, and Rushton (2007) may provide support to this hypothesis. Guterman et al. used a 'CAVE' style virtual reality display with an unrestricted FOV. Although the authors did not measure recalibration they did monitor the walking trajectories of their participants under displaced viewing conditions. It was concluded that walking paths were more consistent with those generated while walking using prisms, rather than those generated while walking with HMDs.

It is worth considering that a possible explanation for the reduction in adaptation with a reduced FOV may not relate to the reduction in exposure to optic flow exposure per se, but instead might be an artefact of the goggles themselves. The introduction of the goggles may have provided observers with a reference frame as to the true position of head-centric straight ahead, in turn reducing the perceived displacement induced by the prisms. This effect is akin to that described in relation to the enclosed environment: a structured environment offers several reference cues as to the true position of the observer (e.g. Beusmans, 1998). Following this line of thought, it is also possible that the frame of the prism glasses themselves provide a reference as to true straight ahead. However, a preliminary analysis of the walking trajectory data revealed that the deviation in walking direction did not differ across the three optic flow manipulations; if the goggles did provide a reference frame as to head-centric straight ahead, an observer should take a straighter path in this condition, which was not found to be the case in our data.

Many of the seminal research papers with regards to perceptual-motor adaptation have reported quite significant degrees of adaptation when an observer's field of view was restricted. For example, in early experiments concerned with adaptation while walking, Redding and Wallace (e.g. Redding & Wallace, 1976; Redding, 1978; Redding, Clarke & Wallace, 1985) restricted participants monocular FOV to only 20°. Additionally, Held and Bossom (1961) binocularly exposed participants to a lateral displacement that afforded a 60° FOV for each eye and were able to obtain quite a substantial amount of visual adaptation.

One major difference between the experiments outlined above and that reported here was the duration of exposure to the optical displacement. Redding and Wallace generally used an exposure time of approximately 10 minutes in all of their walking experiments. Held and Bossom (1961) used exposure times that ranged from 1 hour to 21 hours. In our experiment, exposure was very short, lasting approximately 2-3 minutes. It may well be the case that decreasing the field of view reduces the *speed* of recalibration, rather than the presence of recalibration. Indeed, if it were true that reducing the FOV slows adaptation, this would count as evidence against the reference frame hypothesis. The timecourse of recalibration under conditions of full, intermittent and absent optic flow is explored in Chapter 5. However, the next experiment investigated the role of an error signal in recalibration.

Experiment 3: Does an error signal drive recalibration?

In Held's model, recalibration is driven by an error signal – the discrepancy between anticipated and experienced optic flow. In the above experiments the role of an error signal is assumed; here its role is tested.

In the preceding two experiments, prisms were used to introduce a discrepancy between the anticipated and experienced flow field. In this experiment, we removed the prisms and moved the target. This results in the observer taking a similar trajectory to that taken by prism-wearing observers, in turn experiencing a similar pattern of retinal motion. The important difference is that there is no discrepancy between the anticipated and experienced optic flow. Therefore, there should be no error signal to drive recalibration of perceived direction (see Figure 3.6).

Participants

A total of sixteen right-handed participants were tested in return for course credit. Participants were students who reported normal or correct-to-normal vision (by contact lenses).

Procedure

Using the same environment as in experiment 1 and 2, participants were required to walk towards a series of eight lights mounted at eye level on similar posts to those used as targets in the previous experiments. The experimenter remotely turned on the lights sequentially (see Figure 3.6) and participants were told to walk towards the light that was currently lit. The lights were switched on in a specific sequence to ensure that the trajectories taken matched those taken in experiment 1 for both left and right displacing prisms. Once the observer had travelled a certain distance, the experimenter would turn on the next light in the sequence causing a slight deviation in their locomotor path, and so on, until they eventually reached the opposite side of the area. This was repeated six times for each of the three flow conditions used in experiment 1. To assess the presence of adaptation, measures of proprioceptive and visual straight ahead were taken both prior to walking, and after walking, to the 'moving' light. Also, as in experiment 1, participants were asked to bounce a ball for three minutes between each experimental condition, ordering of the conditions was randomised.

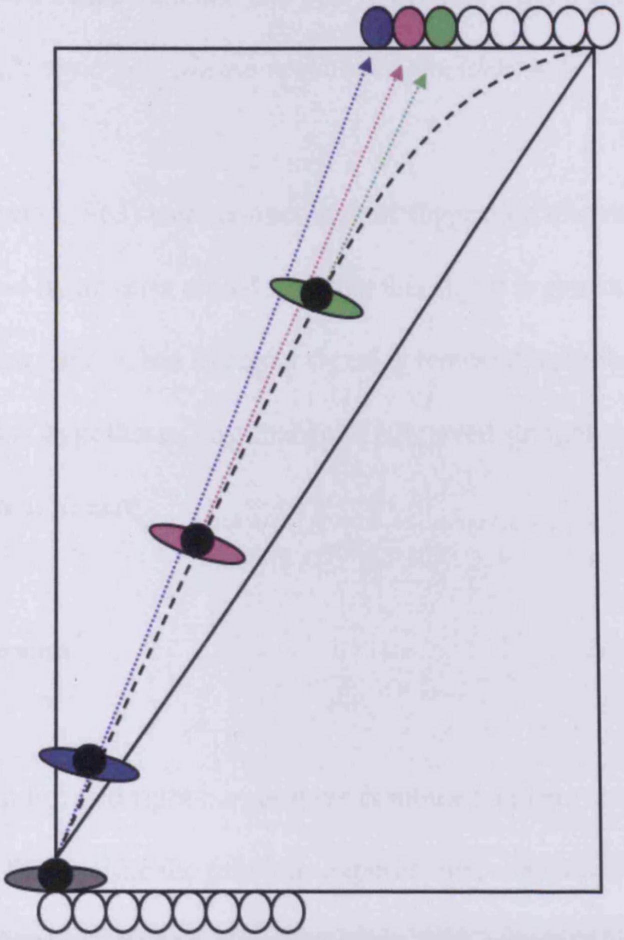

Figure 3.6. Illustration of the light set-up for experiment 3.Here we show the set-up to produce a leftward curving trajectory; the lights were moved to the opposite corners to produce a rightward curving trajectory. The initial start position is shown in grey. The trial would commence when the first light (highlighted here in blue) was switched on – the observer's task was to simply walk towards the light that was on. After a certain distance the next light in the sequence was switched on (pink) causing the observer to adjust their locomotor path accordingly. Each light was switched on once the observer had passed a particular point; in turn causing a curved trajectory that resembled that taken when walking with a misperception of direction (illustrated as a dashed black line). Actual lights used were not coloured, but consisted of a vertical

strip (5cm) of five red LEDs attached to a post at eye level. In comparison to experiments 1 and 2, optic flow always remained coincident with the target.

If Held and Freedman (1963) were correct in their suggestion that recalibration while walking is prompted by an error signal, and that this signal is generated as a result of discrepant optic flow, then when the error signal is removed, recalibration should not occur. Based on this hypothesis, any change in perceived straight ahead should not be significantly different to zero.

Results and discussion

Adaptation for both left and right curves were combined and are shown in Figure 3.7. The figure reveals that, unlike the previous experiments, adaptation is extremely limited across all three conditions. However, there does appear to be a small shift in perceived visual direction that is independent of the optic flow manipulation.

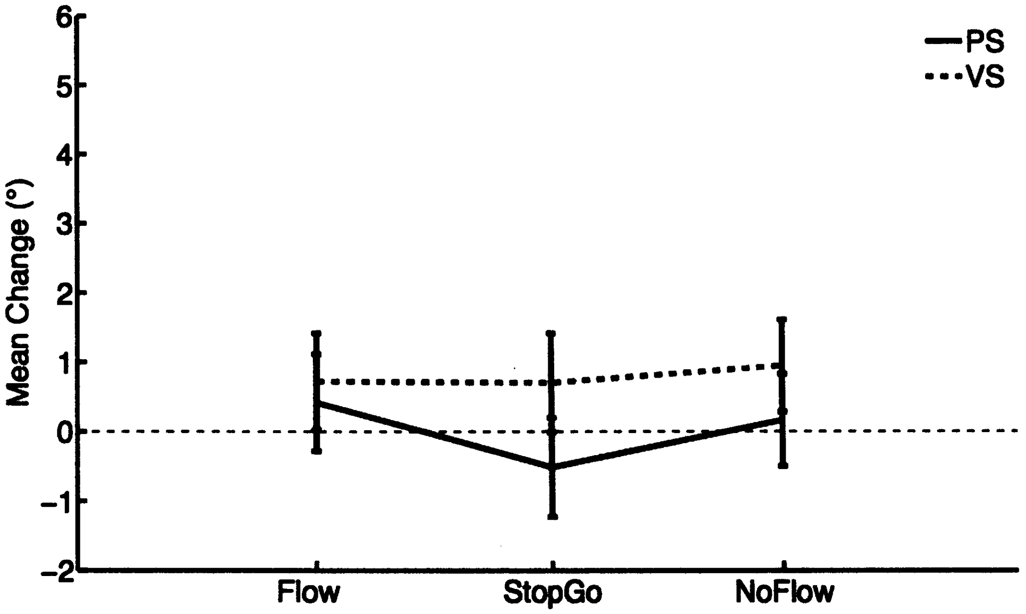

Figure 3.7. Mean level of adaptive shift for both left and right curves combined. Visual shift (VS) and proprioceptive shift (PS) are shown across all three conditions. Error bars = ± 1 SE (within subjects)

To examine whether there was a significant change in perceived straight ahead from pre- to post-walking, a series of one-sample t-tests were conducted to test if the shift in perceived direction was significantly different to 0. Although visual inspection of Figure 3.7 suggests that simply walking on a curved path produced approximately 1° of visual adaptation, only the visual shift in the 'NoFlow' condition was significantly different from zero [t (15) = - 2.277, p < .038]. None of the changes in proprioceptive straight ahead were significantly different from 0.

We can take two things from these results: (i) with no error signal there is no change in proprioceptive straight ahead, and (ii) there is a reduced, but small, change in perceived visual direction. Although the shift in visual straight ahead did not reach statistical significance, it appears that simply walking passively on a curved trajectory is enough to produce a small change in perceived visual direction. Why might this be so? It is possible that when walking on a path that curves rightwards, observers will keep their gaze oriented in a particular direction to maintain fixation on the target. As reported in the introduction sustaining a particular eye posture to one side is likely to produce a small drift in visual straight ahead in the same direction (Paap & Ebenholtz, 1976). Another possibility is that observers turned their head while walking. Research by Grasso, Glasauer, Takei and Berthoz (1996) suggests that while walking on a curved path observers tend to 'go where they look'; changes in head orientation were made before participants changed their walking direction. As highlighted in the introduction, Howard and Anstis (1974) have demonstrated that holding an eccentric head posture can also lead to a drift in perceived straight ahead.

The change in visually perceived direction found in this experiment might thus simply be a result of maintaining an eccentric gaze or head posture for a short period of time. If this is the case, we should also find a small change in perceived visual direction in the absence of optic flow. Indeed, when optic flow was absent (experiment 1) or spatially restricted (experiment 2) we also found a small shift of approximately 1° in perceived visual straight ahead.

It could be argued that the lack of adaptation may not be a result of the absence of an error signal, but is instead a consequence of the introduction of a different element of optic flow. When en-route to a target while wearing prisms, if the observer fixates the target, motion parallax[4] between the target and the immediate surroundings is absent –

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[4] Motion parallax is the relative motion between two objects at different depths within an environment and is an element of the optic field.

the target, and the background, do not appear to move. In the lights experiment, since the target changes, it could be argued that this produces motion parallax between the target and the immediate surroundings. If motion parallax is present then this could explain the lack of adaptation found: there is some evidence to suggest that increasing the saliency of motion parallax reduces the size of curved trajectories taken by prism-wearing observers en-route to a visible target (Rogers & Allison, 1999; Harris & Carre, 2001). However, local motion parallax has never been identified as an important source of information to drive recalibration. Our predictions were based on the more salient cues that might drive adaptation (e.g. simply walking o a curved path, vestibular cues, displaced FoE and proprioception), all of which were held constant in this experiment.

Overall summary and discussion

I have presented strong evidence to suggest that visual motion drives a shift in perceived visual straight ahead: when exposure to visual motion is reduced, the amount of visual adaptation obtained is also reduced. However, while visual recalibration requires optic flow, it appears that proprioceptive recalibration does not. Furthermore, when all else is held equal, but the discrepancy between anticipated and perceived visual motion is removed, *recalibration* does not occur in either perceptual motor system. Although the data does suggest the possibility for a passive component to visual adaptation this trend only reached a level of significance for one condition, and is likely caused by holding a specific eye or head posture.

The results of the three experiments presented here are in line with the hypothesis of Held and Freedman (1963) with regards to the role of optic flow in the recalibration of direction, and to Held's (1961) main contention with regards to the role of an error signal in recalibration. However, they do not speak to Held's (1961) contention concerning the necessity of active (self-generated) vs. passive movement.

The results contrast with the recent findings of Bruggeman et al. (2007). As already noted, the results of the second experiment may explain this discrepancy – it may be due to the restriction on observer's FOV due to the use of HMDs. However, we should note that another possible reason for this discrepancy might be their choice of measure. The choice of using head-target angle as a measure of perceived direction might not pick up a change in the registered position of the head relative to the trunk. Since observers were unable to see their shoulders, it is quite plausible that the position of the head in relation to the trunk was recalibrated. Indeed, evidence from Dolezal (1982) suggests that observers lose track of the orientation of their head under conditions of a reduced FOV. It is also possible that observers assumed that the HMD was not properly oriented on their head, and almost immediately turned their head to compensate for the displacement.

Although Bruggeman did not find a change in their measure of perceived direction, they did find changes in observer's walking trajectories suggesting that perceived direction was recalibrated. Here I have presented data using standardised measures of adaptation to suggest that perceived proprioceptive and visual straight ahead both change in the presence of optic flow, albeit demonstrating opposite relationships. It will be of interest to note whether this trend is revealed in the trajectory analysis –

that is, is there a related decrease in heading error? I will investigate this in Chapter 6. However, in the next chapter I will discuss some more adaptation data concerned with the effect of attentional load.

Chapter 4: The effect of attentional load on the magnitude of recalibration.

In Chapter 3 we demonstrated that adaptation can occur at different locations within the perceptual motor system, and that the location of adaptation can change as a function of exposure to optic flow. In this chapter we aim to investigate the process of recalibration by examining the effect of cognitive load on adaptation while walking. That is, does the detection of discrepant reafferent information require the use of attentional resources?

There is some evidence to suggest that processing optic flow is attentionally demanding. For example Wann, Swapp and Rushton (2000) found that cognitive load significantly affected the accuracy of heading judgements from optic flow. Similarly, Rushton and Rosenthal (2000) demonstrated that level of attention was critical when observers were specifically required to make use of motion parallax (a depth cue that, similar to optic flow, results from motion) while walking with prisms. As outlined in the introduction chapter, Redding and Wallace (1985a; Redding et al., 1985) have examined the effect of a cognitive task on the magnitude of recalibration. The results of their experiment revealed that adaptation decreases as cognitive load increases. This finding is particularly interesting in that it suggests that processing discrepant reafferent information requires attentional resources, which, when depleted, can reduce the magnitude of recalibration.

However, although the findings of Redding and Wallace (1985a) provide insight into the limits of recalibration, their results contradict some of their earlier findings with regards to the magnitude of proprioceptive adaptation obtained; earlier research found little proprioceptive adaptation (similar to our results in the Flow condition of experiments 1 and 2), whereas, using the same environment, their 1985a study found that proprioceptive adaptation significantly exceeded the magnitude of visual adaptation. Below is an overview of the important details across the series of walking studies conducted by Redding and Wallace.

Overview of Redding and Wallace's findings

Redding, Clark and Wallace (1985) initially tested the impact of cognitive load on adaptation by comparing adaptation in a group asked to conduct a secondary task, with a second group who performed no task at all. While conducting the task (or no task), participants were required to wear prism glasses as they walked back and forth along hallways. The main finding was that adaptation was reduced when participants were required to perform the secondary mental arithmetic task. A decrease in walking speed when observers were given a secondary task could not account for the finding of decreased adaptation: when walking speeds were equated, the effect remained.

In a more definitive test of the involvement of attention in recalibration, Redding and Wallace (1985a) varied the level of secondary task difficulty and measured both visual and proprioceptive recalibration. Three levels of task difficulty were used: easy – single digit sums with single digit answers; medium – double digit sums with double digit answers; and difficult – double digit sums with triple digit answers. In line with the original findings it was found that the level of cognitive difficulty of the secondary task paralleled the level of prism adaptation: more adaptation occurred when secondary task demands were minimal. Interestingly, proprioceptive adaptation was found to be substantially greater than visual adaptation across all secondary tasks. This is surprising given the results reported in the preceding chapter: namely, that when optic flow is present (as was the case in Redding and Wallace's experiment), visual adaptation was of a greater magnitude than proprioceptive adaptation.

As mentioned above, research conducted by Redding and Wallace prior to the 1980s revealed a different pattern of results with regards to the relative magnitude of VS and PS; PS was found to be minimal and VS was found to be significantly greater (e.g. Redding, 1973; Redding & Wallace, 1976). To account for this discrepancy Redding and Wallace (1985a) pointed out that in their earlier work the hallway often included noisy human traffic, whereas in their 1985a study the area had been evacuated to prepare for a renovation. According to the directionality of guidance hypothesis (developed in Redding et al., 1985, and discussed in more detail in Redding & Wallace, 1990, and Redding & Wallace, 1997) recalibration is suggested to occur in the system that is being guided: thus, if a particular behaviour is visually guided, recalibration will occur more so within the proprioceptive system and vice versa. Human traffic in Redding and Wallace (1976) was suggested to enhance visual adaptation by providing sound sources and obstacles to prompt non-visual exploration. In the evacuated hallway, such auditory and proprioceptive collisions were largely removed, in turn forcing visual exploration of the environment.

This post-hoc explanation offers an unconvincing account of the different results found, particularly given that there is no way of quantifying just how much observers were using the auditory cues made available in the earlier experiments, exactly what these cues consisted of, or how busy the hallways actually were. Indeed, in the research that found more proprioceptive recalibration (Redding & Wallace, 1985a), sound sources were not completely removed since the experimenter still had to read the mental arithmetic questions out loud to the participant, and extraneous noise came from intrusions from maintenance staff, or from pedestrians wishing to use a bathroom located near the hallway. It is thus unlikely that sound sources can account for the differences in the relative magnitudes of visual and proprioceptive recalibration. If walking is based on egocentric direction (Rushton et al., 1998) then it should be visually guided regardless of extraneous noise. Indeed, the magnitude of visual recalibration was similar in both the noisy (Redding & Wallace, 1976) and non-noisy (Redding & Wallace, 1985a) environments (approximately 2.5° after 10 minutes of exposure), only the magnitude of proprioceptive recalibration changed.

In an attempt to specify particular aspects of the task environment that determine where within the perceptual-motor system recalibration takes place, Redding and Wallace (1985b) conducted a series of walking experiments testing hallway exploration under a number of conditions. The effect of a visible sound source was investigated by having the experimenter read out mental arithmetic questions to the observer while either hidden (following behind the observer) or visible (standing at one end of the hallway). The relative magnitude of recalibration was found to be dependent on whether the experimenter was visible or not: visual recalibration was greater when the experimenter was visible, suggesting that visible sound sources prompt proprioceptive exploration of the environment. In contrast proprioceptive recalibration was greater when the experimenter was hidden from view, suggesting that, in the absence of visible sound sources, exploration of the environment is primarily visual.

However, there is another plausible explanation for these results that contrasts with the directionality of guidance hypothesis: it is possible that the presence of a target (i.e. a visible experimenter) and not a visible sound source per se prompted visual recalibration. Indeed, the same pattern of results was found when the experimenter was visible but did not read out any problems. In the 'visible experimenter' conditions hallway exploration was defined: that is, observers were required to walk along the hallway towards the experimenter and then make a turn behind the experimenter. While doing so, the experimenter quickly moved to the other end of the hall, and the procedure was repeated. When walking towards the experimenter it is likely that participants used egocentric direction, prompting visual realignment. In the absence of a defined target (i.e. when the experimenter followed behind the observer) it is likely that hallway exploration was guided in a different way: essentially it is possible that the participant attempted to maintain a position relative to the corridor walls rather than towards a person (see Donges, 1978).

The results of Redding and Wallace are thus inconclusive with regards to the relative magnitude of visual and proprioceptive adaptation produced after a period of exposure to prisms while walking. The greater magnitude of proprioceptive adaptation found in their 1985a study does not fit with our results reported in the previous chapter, and their account of why proprioceptive adaptation is greater than visual adaptation in the 1985a study is unsatisfactory. Here we used the paradigm of Redding and Wallace (1985a) as a starting point to investigate the relative magnitude of PS and VS, and the impact of cognitive load. Since Redding and Wallace used a hallway environment (which is even more confined than our outdoor environment), and a walking task without a defined target (participants were simply instructed to walk up and down hallways), it will be interesting to determine whether PS is larger than VS, and whether cognitive load impedes adaptation in the same way as described by Redding and Wallace (1985a).

Since we expected attention to reduce adaptation, we extended the exposure time (relative to our previous experiments) to increase the likelihood of finding a change (assuming that the magnitude of adaptation increases with time, e.g. Efstathiou, 1969). To avoid the possibility that a visible 'noisy' experimenter could account for our results, the secondary cognitive task was conducted without any input from the experimenter: that is, observers were required to count backwards rather than complete mental arithmetic tasks read out by the experimenter. Verbal interactions with the experimenter were kept to a minimum: only when observers were stationary at a target with eyes closed did the experimenter speak to give instructions of which target to walk to next. In light of the Redding and Wallace (1985b) results, even though we removed the impact of a visible, talking experimenter, the use of a target should prompt more visual realignment.

The choice of environment meant that noise could not be controlled for. Thus, as in the Redding and Wallace (1976) study, although participants did not physically encounter other people, the environment contained other pedestrians and cyclists, usually students crossing over the environment on their way to a lecture. If Redding and Wallace (1985a) were correct in suggesting that human traffic in the environment can account for the differences in the relative magnitude of recalibration, then we should find more visual than proprioceptive recalibration.

Method

Participants

The 84 participants were right-handed students at Cardiff University. Four participants' data were removed due to problems with the weather. All participants had self-reported normal, or corrected to normal vision by contact lenses only, and were given credit towards a course requirement in return for their participation. Participants were divided into eight groups of ten: forty for each prism deflection (either to the left or to the right), with ten participants in each of the experimental groups (secondary task: difficult, easy, medium, notask)

Procedure

Participants were required to walk from the initial starting point to a target at the far side of the area (see Figure 2.11, Chapter 2) as specified by the experimenter. Upon reaching the target, the participant was asked to close their eyes, and to make a half turn, the experimenter would then indicate which target they were required to walk to next, the participant then opened their eyes and made their way to the specified target. Participants walked back and forth between targets twenty times resulting in a total of forty trajectories.

While walking, participants conducted one of three counting tasks, or were given no task. The counting tasks entailed counting backwards from a given number, in a particular multiple, depending on the level of difficulty. For example, the easy task required participants to count backwards from 300 in 1s, 2s, or from 1000 in 10s, the medium task included counting backwards from 301 in, 4s, 6s, and 11s, and the difficult task included counting in multiples of 13, 14 and 16 from 500. Participants were asked to perform this task out loud so that the experimenter could monitor their progress. The difficulty level of each number was equated in a pilot study prior to the main experiment. Those in the NoTask group were not required to complete any secondary task.

For the pilot study, participants (n=14) each conducted the nine counting tasks used in the main experiment and were given three minutes to complete each task (the order of the tasks was random). The amount of numbers participants were able to count correctly was recorded. Unsurprisingly, participants counted more numbers in the easy tasks and the least amount of numbers in the difficult task. A within subjects ANOVA conducted on the amount of numbers spoken, revealed that the three different tests used to represent 'easy' did not differ significantly from each other ($p = .679$). The same was also found for the medium tests ($p = .287$), and the difficult tests ($p = .213$). When collapsing across the three tests, a within subjects ANOVA found a significant effect of task difficulty [$F(2, 26) = 284.3$, $p = .001$]. To determine whether the three tasks corresponded to three levels of difficulty, Bonferroni post hoc comparisons were used to test for a significant difference between the tasks. All comparisons were found to be significant: easy was significantly different from the medium ($p = .001$), and the difficult task ($p = .001$), and the amount of numbers counted in the medium task was significantly different to those counted in the difficult task ($p < .001$)

In an attempt to ensure that walking speeds were equal across conditions, similar to Redding and Wallace (1985a), participants that received a secondary task were asked to walk at a fast pace, whereas controls were asked to walk slightly slower than their normal walking pace. This was an important manipulation since those completing the counting task were likely to walk slower than those completing no task at all. If this were allowed it could be argued that the faster an observer walks the richer the optic flow information available. To encourage participants to comply with this request they were informed that they were being recorded from above, and that this was to ensure that they were walking at the correct pace.

Results

Figure 4.1 indicates the principle results for the Attention experiment. Deviations above zero indicate an adaptive shift in the correct direction.

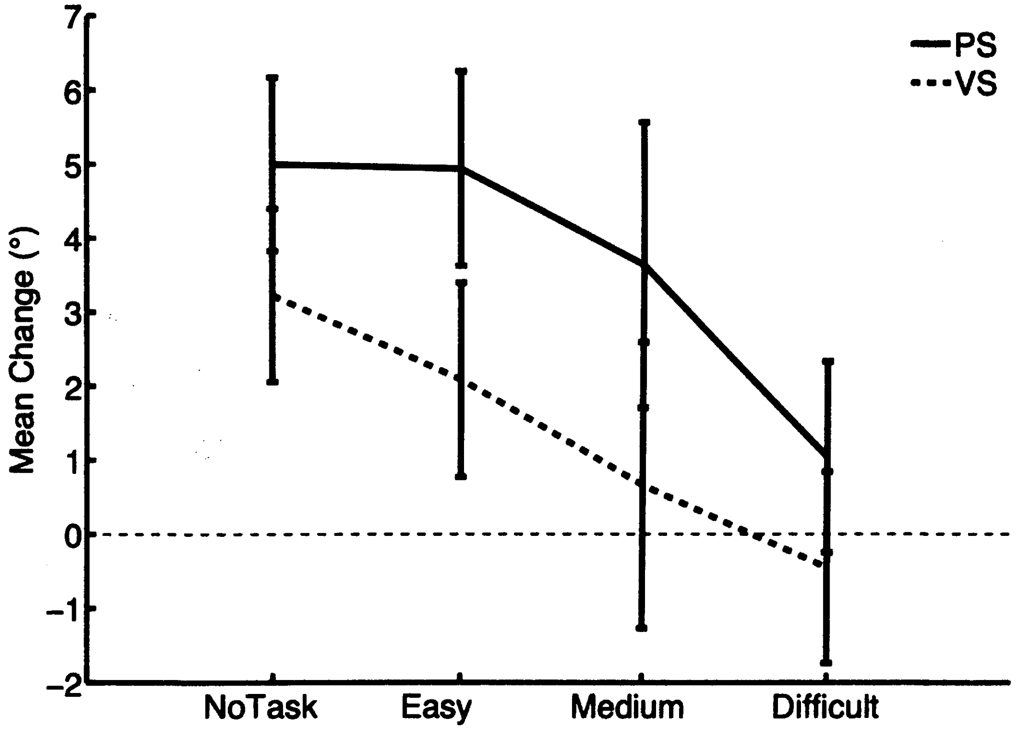

Figure 4.1. Mean level of adaptation for left and rightward displacements combined. Visual shift (VS) and proprioceptive shift (PS) are both shown as a function of four

levels of secondary task difficulty. NB. Error bars = ± 1SE (within subjects), thus are only relevant for comparison within each condition and not between conditions.

It can be seen from Figure 4.1 that, similar to the results of Redding and Wallace (1985a), both visual and proprioceptive adaptation decreased as task difficulty increased. Also similar to Redding and Wallace, the magnitude of PS is much greater than VS across all levels of secondary task difficulty. A mixed measures ANOVA, with condition as the between subjects variable and measure as the within subjects variable, revealed a significant main effect of measure [F (1, 76) = 9.746, p = .003], demonstrating that proprioceptive recalibration was significantly greater than visual recalibration. The main effect of task was also found to be significant [F (3, 76) = 4.484. p = .006] suggesting that a change in cognitive load has a considerable effect on the amount of adaptation obtained. The test also determined that there was a non-significant interaction (p = .850).

Bonferroni post-hoc tests revealed that the significant main effect of task was driven by a difference in adaptation between the notask and difficult conditions (p = .002), and between the easy and difficult conditions (p = .019). When looking at the effect of task on visual and proprioceptive recalibration separately one-way, two-tailed ANOVAs revealed that task did have a marginally significant effect on visual adaptation [F (3, 76) = 2.695, p = .052]. The measure of proprioceptive recalibration was found to violate the assumption of homogeneity of variance and so Welch's F was used (as recommended in Field, 2005). This test revealed a significant effect of task on PS [F (3, 40.182) = 4.162, p = .01].

Despite attempts to keep walking speed constant across conditions, a univariate ANOVA revealed that walking rate was significantly affected by secondary task difficulty [F (3, 76) = 4.916, p = .004] (Figure 4.2). If the imposition of a secondary task causes a general increase in trajectory duration then one would expect to find the longest duration for the most difficult secondary task; however, this is not reflected in the results: post-hoc comparisons using the Tukey HSD test indicated that a significant difference only existed between the notask and medium conditions (p = .001), and not the notask and difficult conditions (p = .224).

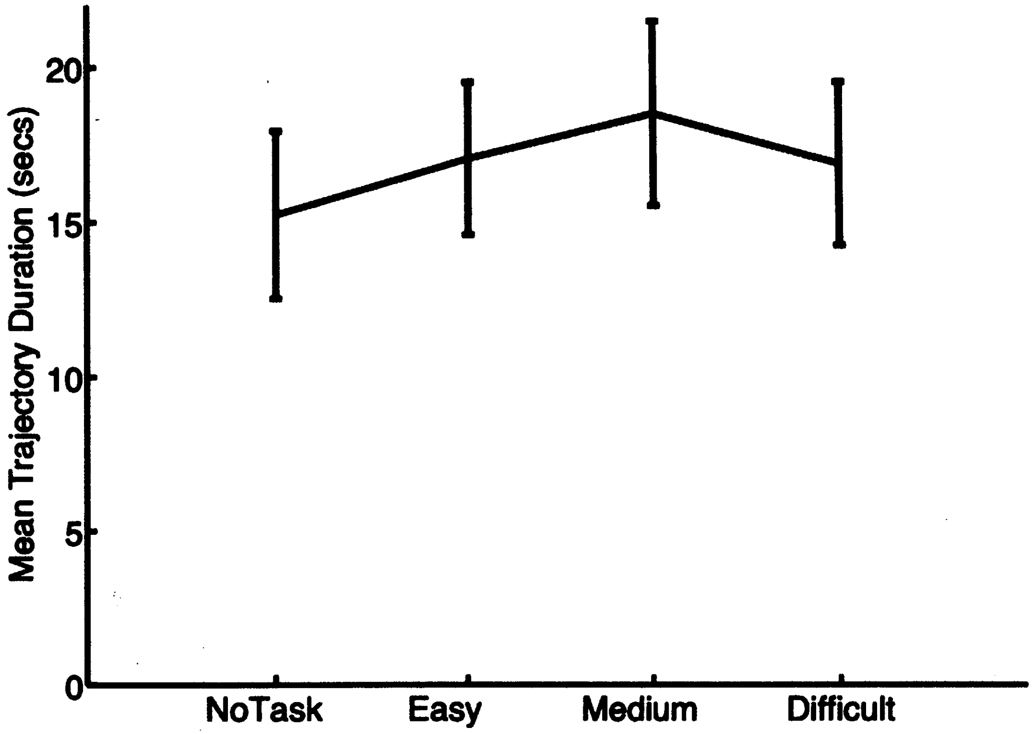

Figure 4.2. Mean trajectory duration as a function of task difficulty for both left and right displacing prisms. Error bars = ±1 SE

It is unknown why walking speed should change be the largest in the medium task condition than in any other condition. However, given the clear recalibration results it is unlikely that walking speed had a significant influence on our data.

Discussion

The experiment presented in this chapter tested the effect of an attentional manipulation on adaptation while wearing prism glasses. It was found that, similar to Redding and Wallace (1985a), PS was larger than VS across all levels of secondary task difficulty and that both proprioceptive and visual adaptation decreased as task difficulty increased. The results demonstrate that cognitive capacity works as a kind of volume control, whereby the magnitude of recalibration can be turned up or down depending on the amount of attentional load imposed on the observer.

An interesting consideration with regards to our results is whether the secondary cognitive task affected the processing of visual information (i.e. optic flow), and, in turn, the detection of an error signal, or whether the error signal was detected but the recalibration process itself was affected. Our results are unable to distinguish between these two possibilities. However, as mentioned previously, there is evidence to suggest that processing optic flow is attentionally demanding (Wann, Swapp & Rushton, 2000). This result points to the possibility that cognitive load interfered with the processing of optic flow; however, another study would have to be conducted to fully investigate this suggestion

Interestingly, the magnitude of recalibration found in our experiment was substantially higher than that found by Redding and Wallace (1985a) even though the power of our prisms was much less: the prisms used by Redding and Wallace displaced the visual array by 17.1°, whereas the power of our prisms was 9°. A possible explanation for this result may relate to the use of a target: having a defined point in which to navigate towards may aid the detection of discrepant optic flow; however, the findings of experiment 2 would suggest that this is only the case if an observer has an unrestricted field of view.

Above we outlined the findings of Redding and Wallace (1976) who demonstrated that, after a similar exposure period, visual recalibration was of a similar magnitude to Redding and Wallace (1985a), and also to the amount of visual recalibration found in the NoTask condition of our experiment. However, the magnitude of proprioceptive recalibration found by Redding and Wallace (1976) was substantially less than that reported in the comparable two studies. Redding and Wallace (1985a) suggested that this discrepancy could be accounted for by 'environment noise' in their earlier experiment prompting proprioceptive exploration of the environment. However, given that proprioceptive recalibration was significantly greater than visual recalibration in our environment suggests that it is unlikely that a noisy environment can account for the difference in results.

The work of Redding and Wallace (1985b) predicted that the use of a target should prompt more visual recalibration that proprioceptive recalibration. However, this was not found to be the case: proprioceptive recalibration was substantially greater than visual recalibration. At a first glance, this result also does not appear to fit with the findings presented in the previous chapter: the notask condition in this experiment and the flow condition in experiments 1 and 2 should be comparable. In experiments 1 and 2 we found that the magnitude of visual recalibration was greater than proprioceptive recalibration. In the comparable notask condition used here, we found the opposite result; proprioceptive adaptation was significantly greater than visual adaptation. This difference could be due to one of three reasons: (i) sampling (i.e. chance); (ii) the difference in design (this study used a between, and not a within subjects, design); or (iii) the time period (here we used 40 trajectories; previously we used 6). The last of these possibilities is the most likely, and potentially interesting. The next chapter will investigate the timecourse of recalibration under conditions of full, intermittent and absent optic flow.

Chapter 5: The effect of exposure time on adaptation

The results presented in the previous chapters have established that the magnitude of visual and proprioceptive recalibration can vary as a function of the available visual information, the presence of an error signal, attentional load and possibly as a function of exposure duration. However, the previous results only give an indication of the magnitude of recalibration at one point in time. Given that it is likely that adaptation develops over the exposure duration, this chapter investigates the magnitude of recalibration at different time points during the exposure period.

Comparisons across experiments suggest different timecourses of visual and proprioceptive adaptation. In Chapter 3 we demonstrated that the magnitude of visual recalibration is greater in the presence of a full optic flow field; however, in a comparable condition in Chapter 4, it was found that proprioceptive adaptation was significantly greater than visual adaptation. Interestingly, in Chapter 3, we also demonstrated that some adaptation could occur in the absence of visual motion, suggesting that the optic flow may speed up, but is not a necessary condition for, recalibration. To investigate the influence of other cues that might aid recalibration (e.g. positional cues, Beusmans et al., 1998), in this chapter we will examine the timecourse of adaptation using the three optic flow conditions of experiment 1: Flow (continuous), StopGo (intermittent) and NoFlow.

Research on the timecourse of adaptation is scant at best. Typically, in earlier studies exposure times of a few minutes during one session were used to measure short-term adaptation (e.g. Held & Gottlieb, 1958; Harris, 1963). Although Redding (1973) and

Redding, et al. (1985), did make some attempt to look at the effect of exposure time on adaptation, by measuring adaptation at fifteen (Redding, 1973), or five minute (Redding, et al., 1985) intervals, only visual adaptation was measured.

One experiment by Hay and Pick (1966) does give some insight into the timecourse of different forms of adaptation. As previously discussed in Chapter 2, Hay and Pick (1966) studied the pattern of changes in several different sensory systems, including eye-head coordination, as well as head-hand and eye-hand coordination, over an extended period of time (see Figure 2.6). With regards to the timecourse of recalibration the results suggested that changes in the head-hand proprioceptive system were much faster than the recalibration of visual straight ahead. Over time, this pattern was reversed with observers demonstrating a decline in proprioceptive adaptation, and a steady increase in visual adaptation, at least until 72 hours of exposure.

In contrast to the findings of Hay and Pick (1966), the results of our previous experiments would suggest that under conditions of full optic flow visual adaptation is a fast process that appears almost immediately: after short exposure times in the NoFlow and FOV experiments, observers exhibited a change in perceived visual direction of approximately 2.5°. In contrast, proprioceptive adaptation was absent under such short exposure durations. Over longer exposure times (as used in the Attention experiment), the magnitude of proprioceptive recalibration was found to exceed that of visual recalibration, whereas the magnitude of visual recalibration was not much greater than that found under shorter exposure times (approximately 0.5° greater).

Although this pattern of results does not fit with that of Hay and Pick (1966), the exposure times used by Hay and Pick were several hours, and even days, longer than those used in our experiments. It may well be the case that the timecourse of recalibration in different sensory systems is much different over shorter exposure durations. Furthermore, the exposure conditions were also very different: we specifically restricted the exposure activity to walking towards a target, whereas Hay and Pick's participants were simply instructed to carry out everyday activities (such activities may have included pointing, looking at their bodies, walking and so on).

The experiment to be reported in this chapter extends the previous results by looking at the effect of exposure time, while also varying exposure to optic flow. Similar to the NoFlow experiment (experiment 1), three exposure conditions are included: full flow, intermittent flow and no flow. Measures of visual and proprioceptive recalibration were taken both before exposure to the prisms, and at four intervals during the exposure period. Using a similar total exposure time to that of the Attention experiment (Chapter 4), observers were required to walk back and forth between targets 24 times resulting in a total of 48 trajectories (an extra eight trajectories than that included in the Attention experiment were used to overcome any de-adaptation that occurred as a function of taking the intermittent measures of recalibration).

As previously suggested, it may well be possible to obtain visual adaptation when optic flow is absent if observers are given enough time to adapt to the optical displacement. If this were the case, we would expect to see a gradual increase in visual adaptation over time, even in the absence of optic flow. The timecourse of proprioceptive adaptation may also differ as a function of exposure to optic flow, such that, it is present almost immediately in the absence of optic flow, but only gradually appears when optic flow is available.

Method

Participants

Three conditions were included, involving a total of sixty-five right-handed healthy participants with normal or corrected to normal vision by contact lenses only. Five participants were unable to complete the experiment due to the weather. All participants were undergraduates at Cardiff University and took part in return for course credit.

Procedure

The experiment consisted of three conditions (flow, intermittent flow and no flow, see Figure 3.1) that varied between participants (20 participants in each group), and four within group exposure phases. The type of prismatic displacement to which participants were exposed (either leftward or rightward displacing prisms) also varied between groups (10 were exposed to base left and 10 were exposed to base right prisms).

As in previous experiments, the trial commenced by taking pre-exposure measures of both perceived visual and proprioceptive straight ahead. There were 48 trajectories in total, and measures of perceived straight ahead were taken prior to initial exposure, and at four different intervals during exposure (after the first 6 trajectories, after the second six trajectories, after 12, and then after 24 trajectories - see Figure 5.1 for an illustration of the order of the procedure). All participants took part in all four phases, and in one of three conditions in which exposure to optic flow was varied. Optic flow exposure was manipulated in the same way as described in experiment 1 (see Figure 3.1, Chapter 3). Participants were guided to the test area by the experimenter, and then back to the exposure area with their eyes closed to prevent de-adaptation between exposure phases.

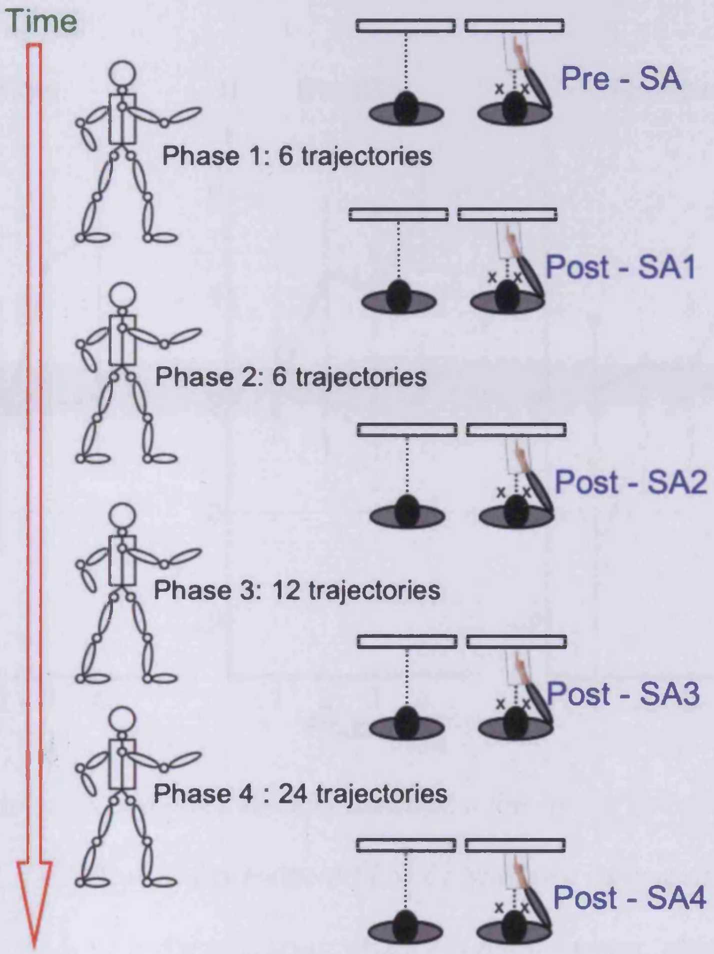

Figure 5.1. Schematic representation of the method used in the timecourse experiment. The procedure consists of four exposure phases that varied in duration. After each phase measures of VS and PS are taken and perceived straight ahead (SA)

is compared with the pre-exposure measures. The same procedure was used in all three exposure conditions (Flow, StopGo and NoFlow).

Results

Figure 5.2 shows both proprioceptive and visual adaptation as a function of time for each experimental condition. The results of experiment 1 are also plotted on the first phase of each condition for comparison.

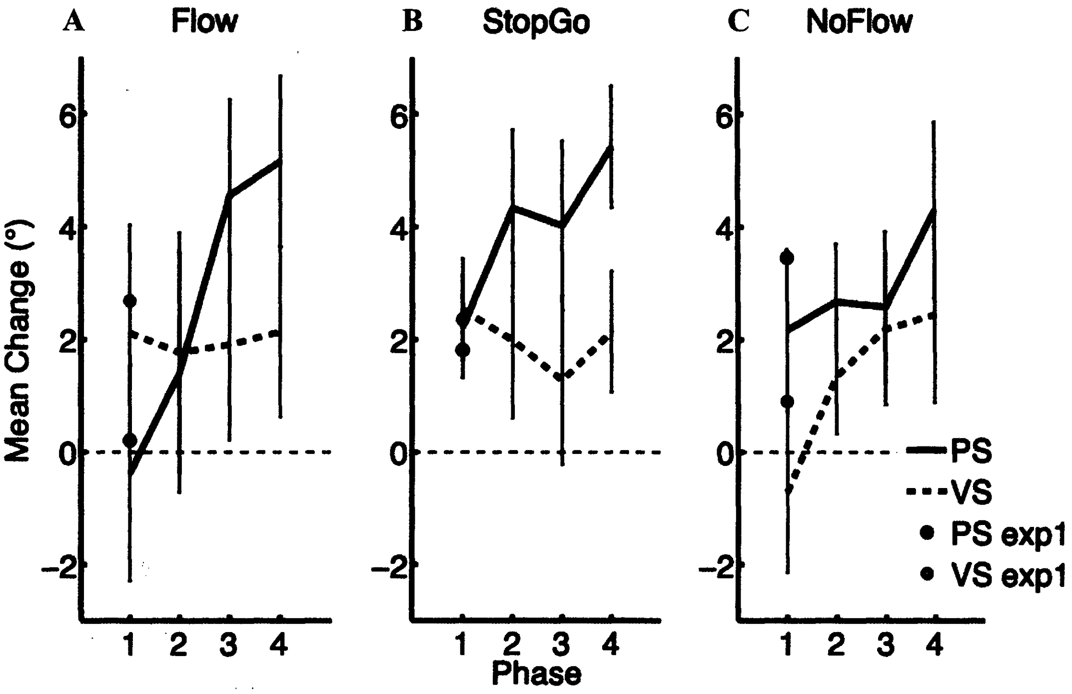

Figure 5.2. Changes in perceived straight ahead as a function of time and availability of optic flow (A: Full Flow B: Intermittent Flow C: NoFlow). Measurement phases were as follows: phase 1 = 6 trajectories; phase 2 = 6 trajectories; phase 3 = 12 trajectories; phase 4 = 24 trajectories. Results are also plotted for the corresponding data from experiment 1. Error Bars = +/-1SE (within subjects)

In line with the results we presented in the previous chapter, and Redding and Wallace (1985a), the general trend suggests a higher level of proprioceptive adaptation across all conditions and exposure phases with just a few exceptions: visual adaptation is higher than PS during phase 1 of the Flow condition, and both PS and VS are at similar levels during phase 2 of the Flow condition, and phase 1 of the StopGo condition. This pattern was also found for the results of experiment 1 plotted in green and blue.

Across time, visual adaptation remains constant in both the Flow and StopGo conditions, and does not exceed approximately 2.5°. Proprioceptive adaptation increases in all three conditions, albeit at different rates. Interestingly, despite a lack of visual adaptation during phase 1 of the NoFlow condition (showing a similar pattern to the results of experiment 1), VS does increase steadily across time, suggesting that in the absence of optic flow, participants were able to recruit other cues to recalibrate visual straight ahead. This is a particularly interesting finding since it suggests that, although optic flow is important for the rapid recalibration of visual straight ahead, given longer exposure times, it is not a necessary condition.

A mixed models ANOVA with exposure time as the within subjects variable, and the availability of optic flow as the between subjects variable, revealed a significant main effect of measure [F (1, 57) = 5.088, p = .028] and time [F (3, 55) = 4.387, p = .008] as well as a significant interaction between measure and time [F (3, 55) = 2.989, p = .041]. This result suggests that the amount of proprioceptive and visual adaptation obtained differs significantly and that this difference changes as a function of exposure time to the optical displacement. From Figure 5.2 it can be seen that the differences are driven by a change in proprioceptive adaptation across time, with little change in visual adaptation, at least for the Flow and StopGo condition.

Individual repeated measures ANOVAs were used to test for the effect of time on both PS and VS in each of the three experimental conditions. With regards to proprioceptive adaptation, time had a significant effect in the Flow condition [F (3, 57) = 4.146, p = .01], and an effect that approached significance in the StopGo condition [F (3, 57) = 2.580, p = .062]. However, the effect of time on PS was not significant in the NoFlow condition (p = .203). Thus, although proprioceptive adaptation does increase somewhat across time when optic flow was absent, this increase was not enough to produce a significant result. This result is interesting in the light of the findings of experiment 1 that suggest that proprioceptive adaptation does not require visual motion; here we have found that PS is restricted in the absence of visual motion. It thus appears that more complete proprioceptive adaptation requires optic flow, or even longer exposure times, than those used in this experiment.

With regards to the effect of time on visual recalibration one way repeated measures ANOVAs revealed that only the NoFlow condition produced results that approached significance [F (1.887, 21.211), = 3.074, p = .061]. Greenhouse-Geisser criteria were used for this comparison since the data violated the assumption of sphericity. Phase did not have a significant effect on visual recalibration in the Flow (p = .937) and StopGo (p = .635) conditions. This result suggests that, in the presence of optic flow, visual recalibration is rapid and asymptotes before the end of phase 1.

With regards to interactions between measure type and condition, the mixed ANOVA found that interactions between measure and condition, time and condition, and the three-way interaction between measure, time and condition were non-significant, yet the latter did approach significance ($p = .087$). Given the almost significant three-way interaction, I would not be confident in stating that the between subjects conditions (the availability of optic flow) did not have an effect on the timecourse of proprioceptive and visual adaptation. Indeed, simply by observing Figure 5.2 one can see that the three-way interaction transpires from the NoFlow condition. In this condition the relationship between time and measure differs from that found in the other two exposure conditions: in the Flow and StopGo conditions repeated measures ANOVAs reveal a significant interaction between measure and time [Flow: $F(3, 57) = 3.645$, $p = .0181$; StopGo: $F(3, 57) = 2.653$, $p = .057$] but this is not the case in the NoFlow condition (p .435).

With regards to comparisons that can be made between this experiment and experiment 1, the results of experiment 1 are plotted alongside phase 1 results for each optic flow condition in Figure 5.2; visual adaptation in green, and proprioceptive adaptation in blue. The main difference between the two experiments was that experiment 1 utilised a within subjects design whereas this experiment used a between subjects design. Despite this, both results still reveal a change in the location of adaptation as a function of the availability of optic flow with more visual adaptation when optic flow is available and more proprioceptive adaptation when optic flow is absent.

Discussion

Building on the findings presented in the preceding two chapters this chapter examined the timecourse of the recalibration process. The results of the experiment presented here reveal that, although it may be the case that visual motion promotes immediate recalibration of visual direction, other cues might be employed over time to enable adaptation. In turn, although visual motion does not drive an immediate proprioceptive adaptation, over time, a change in proprioceptive straight ahead does occur (possibly when a change in visual straight ahead has plateaued).

A possible explanation for the results may be as follows: when there is a discrepancy between perceived and anticipated optic flow, the brain first assumes that an error has occurred in visually perceived direction. In the absence of optic flow, the brain does not have evidence that an error has occurred in visually perceived direction, and so a change occurs in proprioceptive straight ahead. However, over time, sufficient information accrues providing evidence that there is an error in perceived visual straight ahead, and changes in VS start to occur. When optic flow is intermittent both perceived visual and proprioceptive straight ahead are recalibrated, perhaps due to uncertainty within the system as to where the error is. Of course, another explanation of the results could simply be that a change in visual straight ahead, and a change in proprioceptive straight ahead, have different timecourses, and rely on different inputs

One intriguing aspect of the data is that despite the sluggishness of change in felt position over time, proprioceptive adaptation grew to be much larger than visual adaptation. This result contrasts with the findings of Hay and Pick (1966) that suggested an initial shift in proprioceptive direction followed by a decrease in PS, and an increase in change in visually perceived straight ahead. However, as already discussed, Hay and Pick's data was collected over a number of hours and not a number of minutes as we did here. Why proprioceptive adaptation should continue to increase becomes even more perplexing when we consider the results presented in the next chapter, which suggest that proprioceptive adaptation is not related to a change in walking direction during the exposure period (at least when optic flow is present). Based on the data presented above we are unable to answer this question.

The suggestion that, although optic flow is important in the rapid recalibration of visual direction, other cues can be used to drive a change in perceived straight ahead fits quite nicely with some of Bruggeman et al.'s (2007) data. In their experiment Bruggeman et al. (2007) had observers walk to a virtual target in one of two environments in which optic flow was either present or absent. Measuring perceived direction using head orientation, Bruggeman et al. (2007) were unable to find a change in perceived straight ahead during the exposure period. However, as already mentioned there are several problems with this measure that render it an unsuitable representation of perceived straight ahead. When looking at the change in heading error across trials Bruggeman et al. did find a change in walking direction that differed according to the availability of optic flow. On the first few trials, when walking in conditions of rich optic flow, it was found that walking trajectories, although still curved, were much straighter than when optic flow was not available. This finding may be a result of rapid visual adaptation as demonstrated in phase 1 of the experiment presented here.

In Bruggeman et al.'s study, although initial heading error was much larger in the 'post only' environment, in which optic flow was minimal, the error did decrease across trials. The timecourse of this change, however, was much slower than when optic flow was available. A similar change was found in perceived visual direction in our experiment: although the magnitude of visual recalibration is the same in phase 4, regardless of whether optic flow is present or not, recalibration of perceived direction is much faster when optic flow is present (even intermittently so), than when it is absent.

However, although the change in walking trajectories found by Bruggeman do map on to the change in perceived straight ahead demonstrated here, since Bruggeman et al. did not take a formal measure of perceived straight ahead we cannot be certain that perceived visual direction changed in their experiment. An interesting way to examine this idea would be to look at the walking trajectories of observers who participated in the above experiment. This is the aim of the next chapter: Chapter 6 will explore the walking trajectories of participants in the Timecourse experiment, and will thoroughly investigate the relationship between heading error and perceived direction.

Chapter 6: The relationship between perceived direction and heading error

In previous chapters, I have shown that walking while wearing prisms leads to a change in perceived egocentric direction. Displaced optic flow was found to produce a rapid change in perceived visual straight ahead (experiment 1). When optic flow was not available, or was restricted, the initial adaptation occurred within the proprioceptive system (experiments 1 and 2). When optic flow was present, but was not displaced, recalibration did not occur (experiment 3). Over an extended period of time, even in the absence of optic flow, a shift in perceived visual straight ahead was observed (Timecourse experiment). Looking across the experiments it appears that a change in perceived visual straight ahead plateaus at approximately 2.5°, whereas proprioceptive adaptation can reach up to 5°.

The question addressed in this chapter is whether changes in perceived visual and proprioceptive straight ahead are associated with changes in trajectory. Rushton et al. (1998) identified a primary role for egocentric direction in the visual guidance of locomotion (see Figure 6.1). This has been supported in several replications, for example, Rogers and Allison (1999), Rogers and Dalton (1999), and Harris and Bonas (2002). The egocentric direction model is also now included in all models of the visual guidance of locomotion (e.g. Warren et al., 2001). Therefore, it should follow that a change in perceived direction will lead to a change in trajectory. What is unclear is whether a change in trajectory will be a function of a change in visual or proprioceptive straight ahead, or a function of the two. As noted, the magnitudes of visual and proprioceptive recalibration change as a function of exposure time as well as exposure to optic flow. This should thus help us to distinguish between these possibilities.

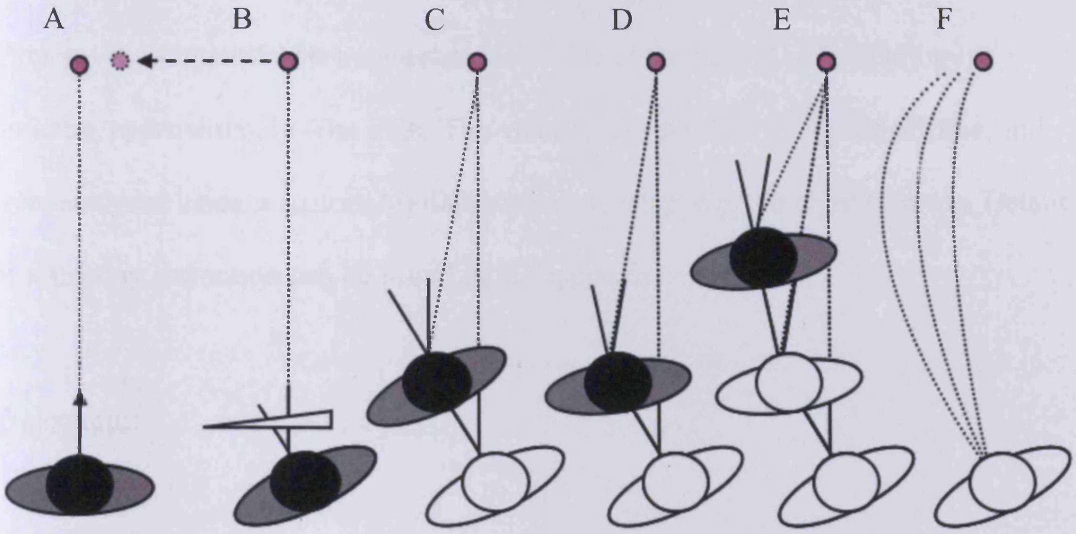

Figure 6.1. Illustration of the predictions of the egocentric direction theory. A: expected trajectory under normal circumstances, without a displacement of perceived direction. B: perceived direction of target when first donning the prisms – the target is perceived to be to the left of true straight ahead, and so the observer adjusts their position accordingly. C: the observer takes one step towards the perceived location of the target. D: as the observer approaches the target, the target will appear to drift rightwards, and so a correction is made in heading direction to keep the target at the same egocentric direction. E: the observer takes another step forward towards the perceived location of the target. F: continuing on their way to the target the observer will continue to make corrective actions as the target appears to drift rightwards, until they eventually reach the target, taking a trajectory in the form of an equiangular spiral. Over time, this curving trajectory is expected to decrease as the observer adapts to the misdirection.

The Data

Participant's trajectories were recorded using a Sony Ex Wave HAD Colour Video Camera (Running at 50 Hz), mounted to the side of the School of Psychology building, approximately 40m high. The videos were digitised using QuickTime, and were analysed using a custom Matllab routine developed by Dr Cyril Charron. Details of trajectory extraction can be found in the appendix.

Trajectories

Figure 6.2 shows the timecourse of the change in target-heading error, taking the mean heading error across the whole trial.

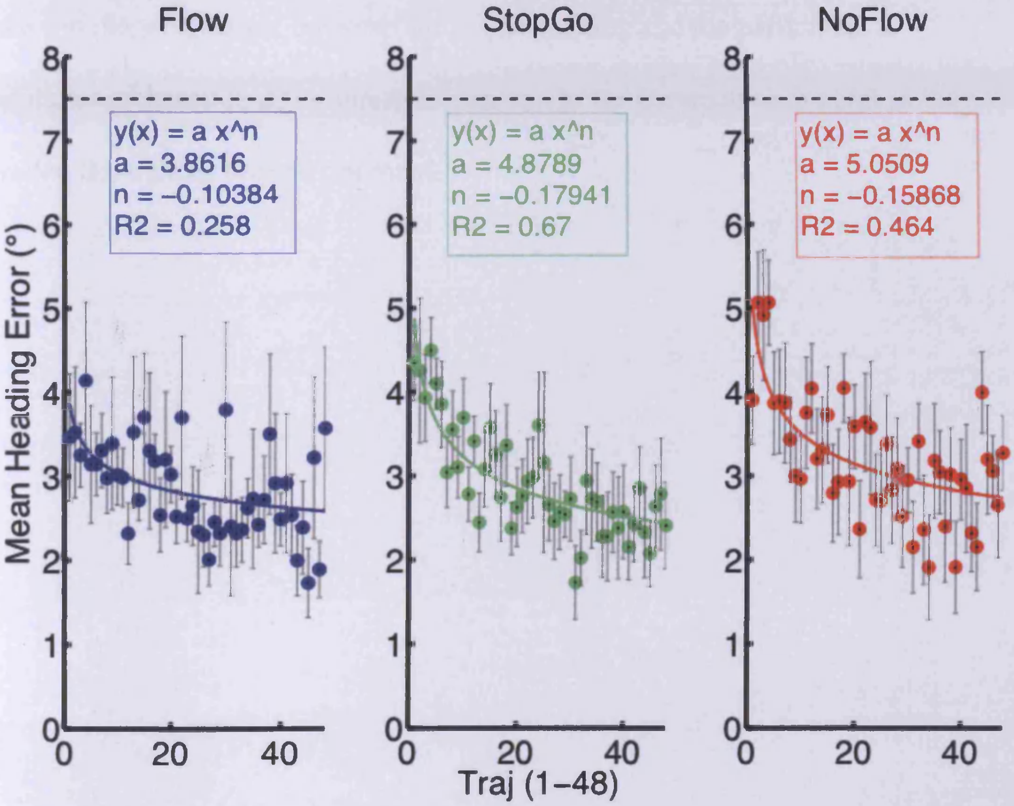

Figure 6.2. Mean heading error for each condition is shown across individual trials. Line fits show a power law fitted to the means. Error bars = ±1 SE

In all experiments there is a decrease in heading error across trials. A power law best described the data, suggesting that in all three conditions heading error initially decreases rapidly, and then begins to plateau. Mean heading error on the first trial of the Flow condition is approximately 1° less than that in the StopGo and NoFlow conditions (α values of 3.86°, 4.89° and 5.05° respectively), although heading error on the last trial in each condition is approximately equal (2.58°, 2.44°, 2.73°).

Figure 6.3 shows the walking trajectories as well as the heading error across the distance of the trajectory. The displayed data represents the mean across the first four (blue line), and last four (red line) trials, collapsing across both right and leftward displacements. Similar to the adaptation results, positive deviations represent a trajectory in the predicted direction. Heading error was calculated by taking the mean of the simultaneous angle between the target position and the participant's instantaneous direction of locomotion (tangent to the curve) at each point as they travelled throughout the environment.

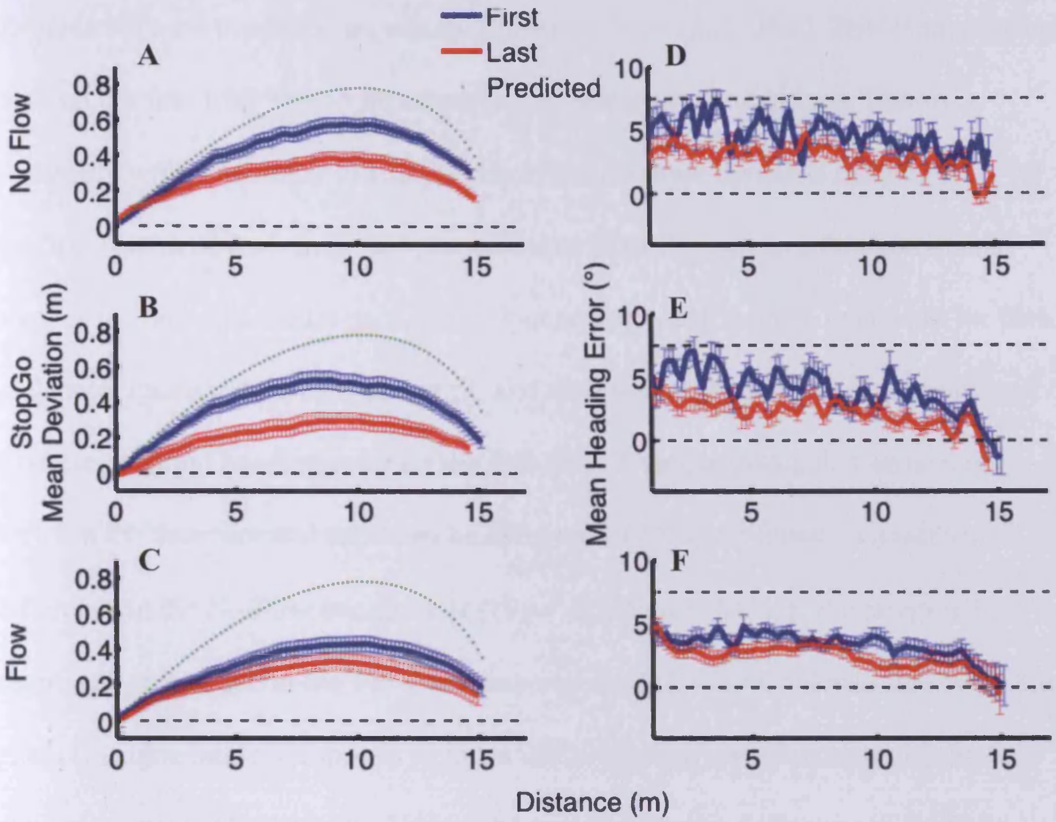

Figure 6.3. A-C: Plan view of the walking paths in each of the three optic flow conditions. Mean paths are shown for the first four trajectories (blue curve) and the last four trajectories (red curve). The green dotted curve corresponds to the predicted trajectory according to the perceived displacement induced by the prisms (7.5 ° - see Figure 2.5). D-F: Mean heading error as a function of distance in the three exposure conditions. The upper dashed line indicates the displacement of the prisms; the lower dashed line indicates a straight trajectory (heading error of 0°). Error bars = ± 1 SE

In all three conditions, participants walked in a curved trajectory to their target (Figure 6.2 A-C), a classic indicator of the involvement of egocentric direction in the visual guidance of walking. The dotted green line highlights the predicted trajectories (7.5°). This prediction is based on the results of the short experiment outlined in Chapter 2 (see Figure 2.5). In all three conditions, the initial deviation does not coincide with the predicted trajectory. Similarly, Figure 6.2 (D-F) shows that heading error on the first trial was approximately 2.5° less than that expected. Due to variability within the data, to analyse this effect, we took the mean heading error on the first 1metre of each trial, and plotted initial heading error as a function of trial number for each individual participant. Rather than using a single data point we fitted each participants data with a power fit, and used the intercept of the line as our best estimate of initial heading error on the first trial. Using one-sample t-tests to test between the intercept and expected heading error (7.5°), we found a significant difference in the NoFlow condition [t (19) = -2.129, p = .047], and a marginally significant difference in the Flow condition (p = .058). Figure 6.4 also illustrates this effect (the blue line corresponds to mean initial heading error across trials). Initial heading error was found to be 75% of the perceived prism deflection in the Flow condition, 91% in the StopGo condition and 80% in the NoFlow condition (the difference in heading error compared to the power of the prisms was 62, 76 and 67% respectively).

The immediate drop in heading error on the first trial cannot be accounted for by exposure to optic flow since heading error is also less than that expected when optic flow is absent. As already described in Chapter 2, this is as we expected: in contrast to those who found first trial heading error to coincide with the displacement of prisms (finding errors of up to 90% of the actual prism deflection, e.g. Rushton et al., 1998; Rogers & Spencer, 2005), we ran our experiments in an enclosed space, rather than in an open environment (see Chapter 2, Figure 2.11). As already suggested in Chapter 2 our enclosed environment provided a variety of alignment and positional cues that have been shown to influence perception of locomotion direction (e.g. Beusmans, 1998; Andersen et al., 2003); such cues are absent in an open environment.

Comparison of first and last trials

Figure (6.3 A-C) illustrates that a reduction in path curvature from the first four to the last four trials was found across all conditions. This pattern of results is also illustrated in the mean heading error data shown in Figure 6.2. Trajectory curvature was found to decrease significantly from the first to the last trial in all three conditions [Flow: t (19) = 2.398, p = 0.27; StopGo: t (19) = 4.007, p = .001; NoFlow: t (19) = 4.126, p = .001]. Interestingly, there is a difference in the magnitude of first trial curvature across the three conditions: lateral deviation on the first four trials appears to be much smaller when optic flow is continuous, compared to when it is intermittent, or absent. Using a univariate ANOVA, this trend was found to approach levels of statistical significance [F (2, 57) = 2.597, p = .085]. Post hoc analyses using Tukey HSD revealed that this effect was driven by a difference in first trial lateral deviation between the 'Flow' and 'NoFlow' conditions (p = .078).

Interestingly, heading error decreased across the course of a trajectory, in most cases reaching 0° at the end of a trial (see Figure 6.3, D-F). Paired t-tests were used to compare heading error on the first 1m of a trajectory to heading error on the last 1m of a trajectory, for both the first four (blue line Figure 6.3) and the last four trials (red line, Figure 6.3). All comparisons were found to be significant (see Table 6.1), according to Bruggeman et al. (2007) this result suggests that participants were adapting during the course of a trajectory.

Condition	Trajectory	df	T	p
Flow	First	19	3.148	= .005
	Last	19	2.880	= .010
StopGo	First	19	3.927	= .001
	Last	19	3.192	= .005
NoFlow	First	19	2.961	= .008
	Last	19	3.666	= .002

Table 6.1. Paired t-test comparisons of heading error at the beginning of a trial compared to heading error at the end of a trial. Results are shown for all three conditions for both the first four and last four trajectories.

However, if heading error at the end of a trajectory is a sign of adaptation, this should be reflected by a significant decrease in the magnitude of heading error on the proceeding trial. Yet, this is not what we, and others (Bruggement et al. 2007), have found. Heading error at the beginning of a trial was always much greater than heading error at the end of a trial (even when comparing between the first four and last four trials of the entire condition). Unfortunately, without the necessary control conditions we can only make speculations with regards to this effect. It could be possible that observers switch to an optic flow based visual guidance strategy the closer they get to the target, thus trajectories are straighter because observers are not using egocentric direction to guide their walking paths (see, Bruggeman et al., 2007). However, if this were the case one would not expect heading error to decrease in a continuous fashion until the end of the trial – the switch to the use of optic flow for the visual guidance of walking should be reflected by a sharp decline in heading error at some point closer to the beginning of the trial. We would propose a more plausible explanation relating to the number of cues available as the observer gets closer to the target: for example, at larger distances target drift is absent (e.g. Rogers and Spencer, 2005); furthermore, since the target was closer to the surrounding walls of the environment, as the observer approached the target more positional cues were available, and this may have produced a straighter walking path. It is also possible that en-route to the distant target, the build of optic flow enabled fast recalibration on that specific trial.

To test for these possibilities it would be worthwhile conducting a control experiment requiring observers to start at different distances from the target object. Would heading error at a distance of 7 meters from the target be the same if observers started at 17 metres compared to a starting distance of only 8 metres? If positional information were influencing heading direction one could hypothesise that yes, heading error would be the same. If the build up of optic flow were important then one could predict that heading error would be different in the two starting distances conditions.

With regards to adaptation in the initial heading error (first 1m of a trial) we performed a similar analysis to Bruggeman and colleagues (Bruggeman et al., 2007; Bruggeman & Warren, 2010). Since the initial heading error at the onset of a trial reflects the mapping between target direction to initial walking direction, a change in initial heading error can be taken as evidence that an observer is using egocentric direction to guide locomotion. Figure 6.4 shows the change in initial heading error (blue), and heading error at the end of a trajectory (last 1m), across all 48 trials.

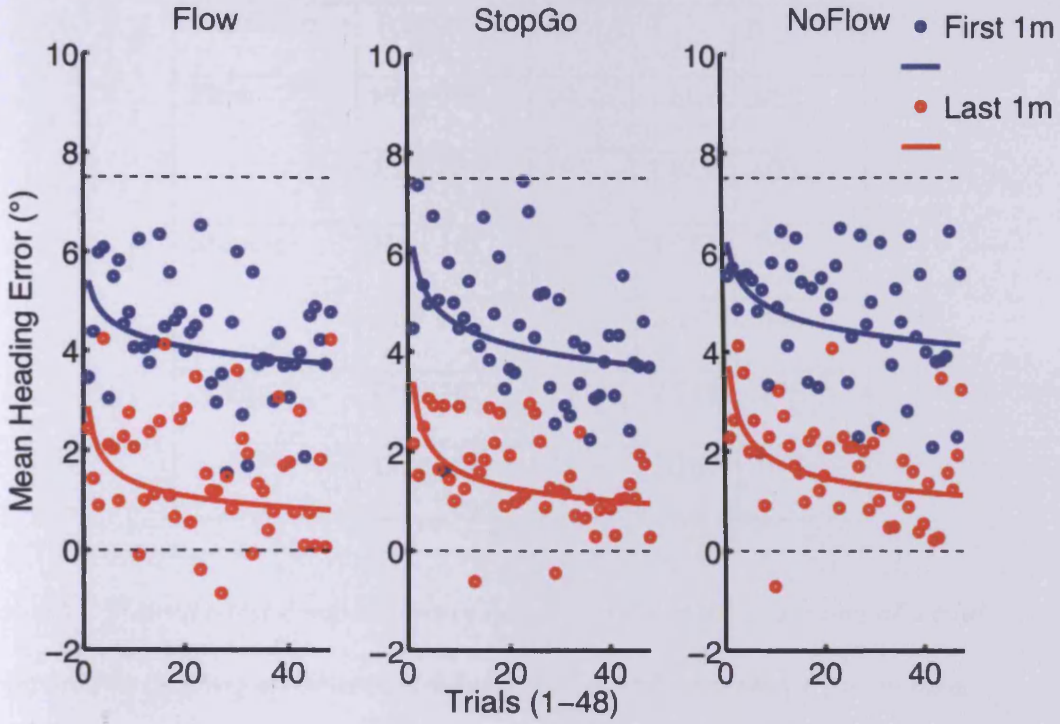

Figure 6.4. Mean initial target-heading error for the first 1 metre (blue) and last 1 metre (red) of a trajectory is shown across all 48 trials. Data is fitted with a power law.

To test if there was a significant decrease in heading error across trials (both initial heading error – first 1m – and heading error at the end of each trajectory – last 1m) we fitted each participant's data with a power law. Similar to the analysis conducted above, because of sampling noise, rather than relying on a single data point (the first trial), we used the line fit to provide the best estimation of heading error on trial one and trial 48. A series of t-tests were conducted. To test for a decline in initial heading error (first 1m – blue line) across trials, heading error on trial 1 was compared to heading error on trial 48 for all three conditions, the same comparison was also made between heading error at the end of a trajectory (last 1m – red line). The results of the 6 tests are shown in Table 6.2.

Condition	Trajectory	df	T	p
Flow	First 1m	19	1.801	.088
	Last 1m	19	1.911	.071
StopGo	First 1m	19	3.013	.007
	Last 1m	19	2.115	.048
NoFlow	First 1m	19	2.314	.032
	Last 1m	19	2.167	.043

Table 6.2. Paired t-test comparisons of heading error at the beginning of a trial compared to heading error at the end of a trial. Results are shown for all three conditions for both the first four and last four trajectories.

The statistics revealed that target-heading error on the first 1m of a trajectory significantly decreased from the first to the last trial in all three conditions; however, in the Flow condition this effect was only found to be marginally significant. In line with Bruggeman and Warren (2010), the results demonstrate adaptation in the initial walking direction. Why this effect should be less pronounced in the Flow condition is surprising, and may simply be a reflection of the large variability in the data. Below we consider whether this change in target-heading error can be mapped onto a change in perceived straight ahead.

The relationship between heading direction and perceived straight ahead

To assess whether a change in perceived direction maps onto heading error, I will consider the change in heading across each exposure phase. Change (relative to baseline) in straight ahead was measured after trials 6, 12, 24 and 48; we attempted to produce comparable measures for change in target-heading angle. It has been demonstrated that exposure to optic flow produces a rapid recalibration of visual straight ahead (Wu, He & Ooi, 2005). This poses a problem. If we use the first trial for the Flow and StopGo data as a baseline for estimating change in trajectory, due to the optic flow, it is likely that the baseline will be contaminated by fast acting changes in perceived straight ahead experienced during the course of the first trial. We concluded that the best way to estimate the walking trajectory without adaptation is to use the first trial of the NoFlow condition. Therefore, in the analysis that follows, the first NoFlow trial serves as our baseline. Similar to the analysis conducted above, because of sampling noise, rather than relying on a single data point (the first trial) we used the intercept of the line fit for trials 1-6 (phase 1) as the best estimate of initial heading without any adaptation.

Similar considerations drive our choice of the estimate of target-heading angle at the time that the measures of visual and proprioceptive straight ahead are taken. When the observer stops to perform the VS and PS tasks it is likely that there is a small loss of adaptation. To overcome this, we bracketed the measures of perceived straight ahead by taking the mean of the heading error on the two trajectories proceeding the VS and PS measures, and the two trajectories immediately after. First trial heading error was thus compared with the mean heading error on trials 5-8, 11-14 and 23-26. Because there were no more walking trajectories after the final VS and PS measure, we were unable to estimate mean target-heading angle on the 48th trial.

Predictions

Whether perceived visual direction or perceived proprioceptive direction, or both, should influence heading error is unknown. Reafferent visual information provides an error signal indicating that there is an error somewhere within the perceptual motor system, it does not provide information as to where the error is. When comparing recalibration with the change in heading error I will thus examine all three representations of perceived direction.

Consider the results of the 'Flow' condition of the Timecourse experiment presented in the previous chapter. The magnitude of visual recalibration remains constant across the four experimental phases, whereas proprioceptive adaptation continues to increase. If the change in walking direction is due to a change in perceived visual direction, then the difference in target-heading error measured against baseline should be comparable (in the order of 2.5°). In contrast, if the change in walking direction is due to a change in perceived proprioceptive straight ahead, then the difference in heading error compared to baseline should increase and reach approximately 5°.

The results

Figure 6.5 shows the outcome of the comparison between changes in perceived straight ahead and changes in target-heading error. For reference, the data from experiment 1 (NoFlow experiment) is also plotted on the graphs. This data is comparable to phase 1 of the Timecourse experiment since it contained the same number of trajectories, the same number of participants, and the same three exposure conditions. The primary difference was that it was a within subjects design, as compared to a between subjects design (used in the Timecourse experiment).

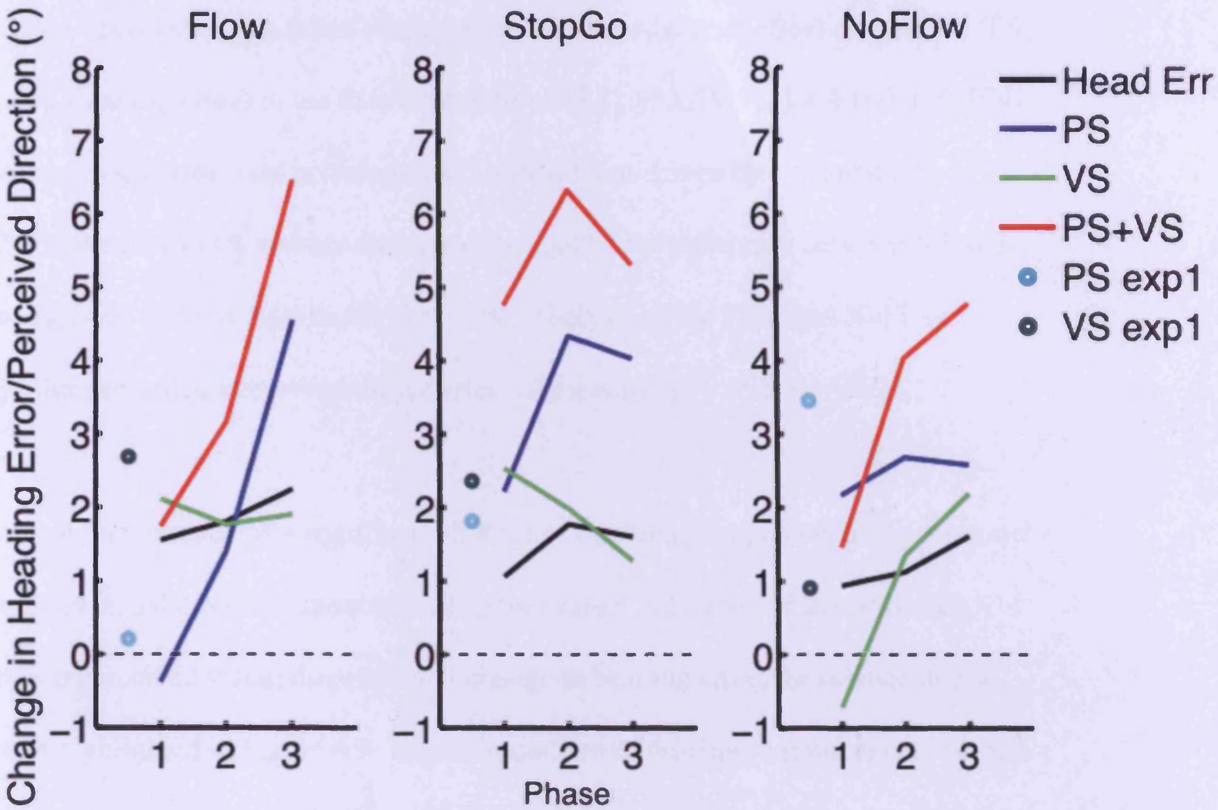

Figure 6.5. Change in heading error in degrees from the first of the NoFlow trials (best estimate of heading error without any adaptation) to the last trial for phases 1, 2 and 3.To represent heading error on the last trial of a phase, the mean of the last two trials and the first two trials of the subsequent phase was taken to overcome the potentially disruptive effects of measuring perceived straight ahead. Mean change in perceived direction (visual, proprioceptive and total – PS+VS) from pre- to post-exposure is also displayed for comparison. PS and VS are also shown from experiment 1 (PS in cyan and VS in a dark green).

Visual inspection of Figure 6.5 demonstrates that PS and PS+VS are clearly too large, and of the wrong gradient, to account for the change in heading error. The change in perceived visual direction is of the correct magnitude and fits well with seven of the nine data points (the discrepant points being trials 5:8 in the StopGo and NoFlow conditions). Statistical analysis on each exposure condition using repeated measures

ANOVA revealed a significant (Greenhouse-Geisser adjusted) effect or measure (PS, VS and Heading error) in the StopGo condition [F (1.553, 29.503) = 4.160, p = .034]. Bonferroni post-hoc tests revealed that this effect was driven by a significant difference between PS and heading error (p = .042); the difference between VS and heading error was not significant (p = .304). Analysis of the Flow and NoFlow conditions revealed a non-significant effect of measure (p = .196; p = .991).

Although the absence of a significant difference between change in heading error and change in visual direction cannot be taken as a direct indication of a relationship between perceived visual direction and change in heading error, the relationship is further highlighted in Figure 6.5. Visual inspection of this figure immediately reveals that a change in heading error from the first to last trial can be mapped quite nicely onto a change in visual straight ahead. Although this was only found to be statistically significant in the StopGo condition, the statistics for the Flow condition did approach significance. Interestingly, the results thus hint at the possibility that there is a relationship between VS and heading error only when optic flow is available.

Summary and discussion

The aim of this chapter was to determine whether the changes in egocentric direction presented in Chapter 5 were related to a change in heading direction. Since egocentric direction is a primary cue in the control of locomotor direction (Rushton et al., 1998), it was predicted that a change in perceived direction would map onto a change in heading error.

Analysis of the walking trajectories revealed a significant change in initial heading error from the first to the last trial in all three exposure conditions. This result lends support to the hypothesis that observers were using perceived direction to guide their walking. We also demonstrated adaptation in the ongoing walking trajectory (target-heading error decreased during the course of a trajectory); in the Flow condition this finding is compatible with the hypothesis that optic flow is used to directly guide locomotion (e.g. Warren et al., 2001); however, the finding of ongoing adaptation when optic flow was not available does not fit with this suggestion, and instead points to the use of environmental cues to aid recalibration.

When examining the relationship between heading error and recalibrated proprioceptive and visual direction, we found a change in both perceived direction and heading direction. The trends present in the data suggest that a change in perceived visual direction captures the change in target-heading error quite nicely, and that this relationship is more prominent in the two conditions where optic flow is available (Flow and StopGo).

Very little previous research has looked specifically at a relationship between a change in perceived direction and a change in heading error. Some have looked at the change in heading error over time as a way of measuring a change in perceived direction (e.g. Rogers & Spencer, 2005). However, a change in walking direction can only be interpreted as indirect evidence of a change in perceived direction.

As discussed in the previous chapter Bruggeman et al. (2007) measured both a change in heading direction, and a change in perceived straight ahead. The change in heading error found in their experiment ties in quite nicely with our recalibration data presented in Chapter 5: recalibration is greater and more rapid in the presence of optic flow. This finding also fits with the trajectory deviation data shown in Figure 6.3 A-C. However, although the results of Bruggeman et al. demonstrated a change in heading error, unlike our results, this change did not map onto a change in their measure of perceived direction. On the basis of this, Bruggeman et al. concluded that the change in observers' behaviour was not driven by a change in perceived visual straight ahead, but was a product of recalibrated visuo-locomotor mappings.

However, as previously discussed, Bruggeman et al.'s (2007) measure of perceived direction is problematic: using head orientation in relation to the target position only takes into account one component of recalibration. If an observer experiences a change in registered eye position, then you might expect a change in head orientation in relation to the position of the target. In contrast, if the registered change in perceived direction occurred between the head and the trunk, then measuring the direction of the head relative to a target would not reveal a change. Indeed, it is likely that a change in head-trunk orientation did occur in the Bruggeman et al. experiment: when taking their first step, observers would realise that they were not going where they expected, and consequently change the orientation of their head. As a result of wearing HMDs, and not prisms, participants were unable to see their shoulders, and so may perceive their head as being straight when it was actually turned to the side.

A discrepancy in felt head position is likely to occur when wearing a HMD due to the weight of the device, and the potential that the device is not properly aligned with the observer's head. Dolezal (1982) reported that when FOV is restricted, observers very rapidly lose track of the orientation of their head. Recalibration in the Bruggeman et al. study is thus more likely to occur between the neck and the trunk since participants would very rapidly attribute any error to a mis-oriented head, and change their head posture accordingly. In this sense it might be more appropriate to measure a change in head orientation in relation to the torso, and not relative to a target.

In contrast to Bruggeman and colleagues (Bruggeman et al., 2007; Bruggeman & Warren, 2010), Morton and Bastian (2004) used standard measures of perceived visual and proprioceptive direction to measure a change in perceived direction. However, similar to Bruggeman et al., they were also unable to find a significant change in perceived straight ahead (1.07° shift in visual straight-ahead and 0.79° change in proprioceptive straight ahead), yet did find a change in walking trajectory. Morton and Bastian concluded that this change in walking direction was a result of recalibration within "some aspect of the motor command" (p2507). However, it is possible that the exposure task could account for the lack of change in perceived direction: rather than walking towards a target, participants were required to walk with their arms crossed while remaining within boundary lines (see Donges, 1978).

Unlike previous results, we were able to demonstrate a *direct*[5] relationship between a change in perceived direction and a change in target-heading error. Specifically we found that a change in visual straight ahead in particular can be mapped onto a change in walking direction.

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[5] . The use of the term 'direct' does not specify a direction of causality. However, it is noted that although it is easy to see how direction could affect locomotion it is not obvious how it could work the other way round.

Chapter 7: Prism adaptation asymmetry and its relation to heading error

Research concerning adaptation to a visual displacement often incorporates a combination of left and rightward displacing prisms (e.g. Hay & Pick, 1966; Bruggeman & Warren, 2010), or includes only one direction of displacement (e.g. Bruggeman et al., 2007; Morton and Bastian, 2004). The choice of which displacement direction to use is generally thought to be only a trivial matter. This approach is apparently legitimised by early research suggesting that displacement direction does not have a differential effect on adaptation (e.g. Rekosh & Freedman, 1967; Wallach & Huntington, 1973). However, there is a hint in the literature that there might be a difference in the magnitude of recalibration obtained from left and rightward displacing prisms (Efstathiou, 1969). In analysing our adaptation results we noticed that there might be a left/right difference, and so decided to investigate this further.

Recently, the idea of an effect of displacement direction has been revived, with findings suggesting that the direction of the optical displacement may indeed have an important impact on the magnitude of adaptation. Research by Michel, Vernet, Courtine, Ballay and Pozzo, (2008) sheds some light on adaptation asymmetry. Michel et al. investigated the effect of optical displacement direction on adaptation during pointing and walking exposure. To measure recalibration observers were required to complete a goal oriented locomotor task (turn and face a target, close their eyes, and walk towards it) and a manual-pointing task (point with eyes closed to a previously seen visual target). The tasks were completed both prior to and after either a period of pointing or walking exposure. Unfortunately, measures of visual and proprioceptive straight ahead were not taken, and heading direction while walking was not recorded.

With regards to an asymmetry in the magnitude of recalibration, when adaptation was measured using a pointing aftereffect task, Michel et al. did not find any significant differences between left and rightward displacements – this was the same for both pointing and locomotor exposure. When measuring adaptation using a locomotor task Michel et al. found an asymmetry in the magnitude of adaptation; finding more adaptation after exposure to a leftward displacement. However, this asymmetry only occurred after participants were exposed to the prisms while conducting a pointing task, and not while walking.

Why would adaptation while pointing produce an asymmetry only when measured using a locomotor task?

Michel et al. (2008) explain the asymmetry demonstrated in their data by referring to a different type of adaptation: that is, they suggest that 'cognitive' adaptation adds to sensorimotor aftereffects but only for leftward prisms. In an earlier review Michel (2006) contended that the cerebral plasticity involved in adapting to leftward displacing prisms affects spatial cognition, perhaps by enhancing plasticity in the left cerebellum, to weaken activity in the right hemisphere. Michel et al. (2008) suggested that, as a result of weakened right-hemisphere activity, leftward adaptation induces a neglect-like bias in space representation, causing an over-representation of the right side of space.

Michel et al. (2008) suggested that only the locomotor aftereffect task (face a target, close eyes, walk towards the target) revealed this cognitive aftereffect because it required participants to hold a representation of the target position in memory. Since pointing towards a remembered target position is much faster than walking towards a target, it was suggested that a representation of the target was not held in memory for sufficient time to reveal a 'cognitive' aftereffect. With regards to why this asymmetry should only occur for pointing exposure, and not locomotor exposure, Michel et al. suggested that, since participants did not directly look at their feet while walking, the detection of sensorimotor discordance was likely to be weaker in the locomotor task.

Others have also found greater adaptation after exposure to a leftward displacement. For example, Colent, Pisella, Bernieri, Rode and Rossetti (2000) used the line bisection task, whereby an observer is asked to indicate the mid-point of a horizontal line, to assess asymmetries in adaptation. Observers demonstrated an aftereffect after a period of pointing while wearing leftward, and not rightward, displacing prisms; they perceived the centre of the line to be further rightwards. Bultitude and Woods (2010) also found a similar effect using navon stimuli. Navon stimuli are figures in which small letters are arranged so that they form a large letter. In healthy participants these stimuli are generally processed globally, such that observers will primarily respond to the larger letter and not the smaller letters. Bultitude and Woods found this bias towards global processing was reduced only when observers underwent a pointing procedure while exposed to leftward displacing prisms, and not rightward displacing prisms.

In light of the conclusions of Michel et al. (2008) aftereffects should be symmetrical if the exposure task does not allow sufficient detection of a sensorimotor discordance, and the aftereffect task does not contain a cognitive component. Based on the magnitude of adaptation found in our walking experiments it is safe to say that our walking exposure paradigm allowed for sufficient detection of sensorimotor discordance. However, it is not likely that this discordance detection was conscious; observers were unaware that they were not walking straight. Our exposure task differed substantially to that used by Michel et al: we asked observers to walk directly towards a target whereas Michel et al. asked observers to walk around the outline of a rectangle (4m x 5m) while maintaining a distance of 30cm. Thus, if our measures of perceived direction contained a cognitive component, then aftereffects should be larger after exposure to a leftward displacement.

In part 1 I will first consider whether any asymmetries exist in the magnitude of recalibration found in the experiments presented in Chapters 3-5 (NoFlow, FOV, Error Signal, Attention and Timecourse). In part 2 I will examine whether a similar asymmetry exists in the trajectory data of the Timecourse experiment (presented in Chapter 6).

PART 1: Asymmetries in adaptation measures

In the preceding chapters the discussion of adaptation was concerned with the combined data collected for left and rightward displacements. In this section I will investigate if any asymmetries exist in the magnitude of adaptation obtained after exposure to left and rightward displacing prisms. Figure 7.1 reveals adaptation obtained in experiments 1-3 (NoFlow, FOV, Error Signal), partialing out displacement direction.

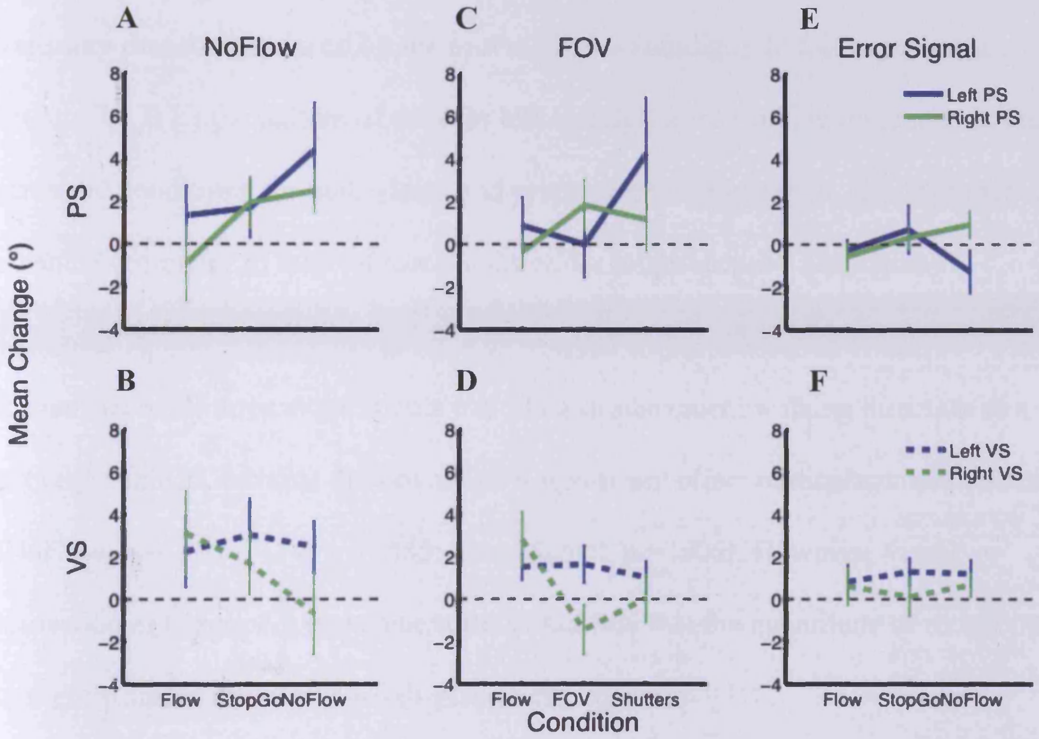

Figure 7.1. Differences in adaptation as a function of displacement direction. The top row corresponds to asymmetries in proprioceptive adaptation (PS); the bottom row shows left/right differences for visual adaptation (VS). In the Error Signal experiment Left/Right refers to walking on a leftward vs. rightward curve. Error bars = ± 1 SE.

With regards to adaptation in the NoFlow experiment (Figure 7.1 A B), the general trend suggests that visual adaptation decreases as exposure to optic flow decreases (Flow – StopGo – Noflow) for both left and rightward optical displacements. In contrast, proprioceptive adaptation increases as the availability of optic flow decreases for both displacement directions. This reiterates the trends found in the combined data analysis presented in Chapter 3. For the FOV experiment (experiment 2 – Figure 7.1 B C) we get a similar pattern of results: both displacement directions show a decrease in visual adaptation, and an increase in proprioceptive adaptation, as exposure to optic flow decreases. Left/right in the Error Signal study refers to the trajectory deviation induced by the moving lights paradigm. In this experiment (Figure 7.1 D E) the pattern of data for left and rightward walking directions is similar across all conditions for both visual and proprioceptive adaptation, although there is a notable asymmetry in the NoFlow condition for proprioceptive adaptation.

Reanalysis of all three experiments including displacement/walking direction as a between subjects variable did not reveal a significant effect of displacement direction (NoFlow, $p = .357$; FOV, $p = .455$; Error Signal, $p = .906$). However, visual inspection of Figure 7.1 does hint at the possibility that the magnitude of recalibration is slightly higher after leftward displacement exposure.

In experiment 1-3 observers were exposed to the displacement for only a short period of time. The next two sections explore asymmetries in the Attention experiment (Chapter 4) and the Timecourse experiment (Chapter 5) where exposure times were much longer.

The effect of cognitive load

In the Attention experiment (Chapter 4) a between subjects design was used such that participants were required to complete one type of secondary cognitive task while walking. The tasks involved counting backwards and, based on the results of a pilot study, were deemed as easy, medium or difficult to complete. A fourth group did not complete any task at all. The combined results (including both left and right prism data) suggested that, similar to Redding and Wallace (1985a), the magnitude of recalibration decreased as the difficulty of the secondary cognitive task increased. This was found for both visual and proprioceptive recalibration. Figure 7.2 shows the same data separated according to displacement direction.

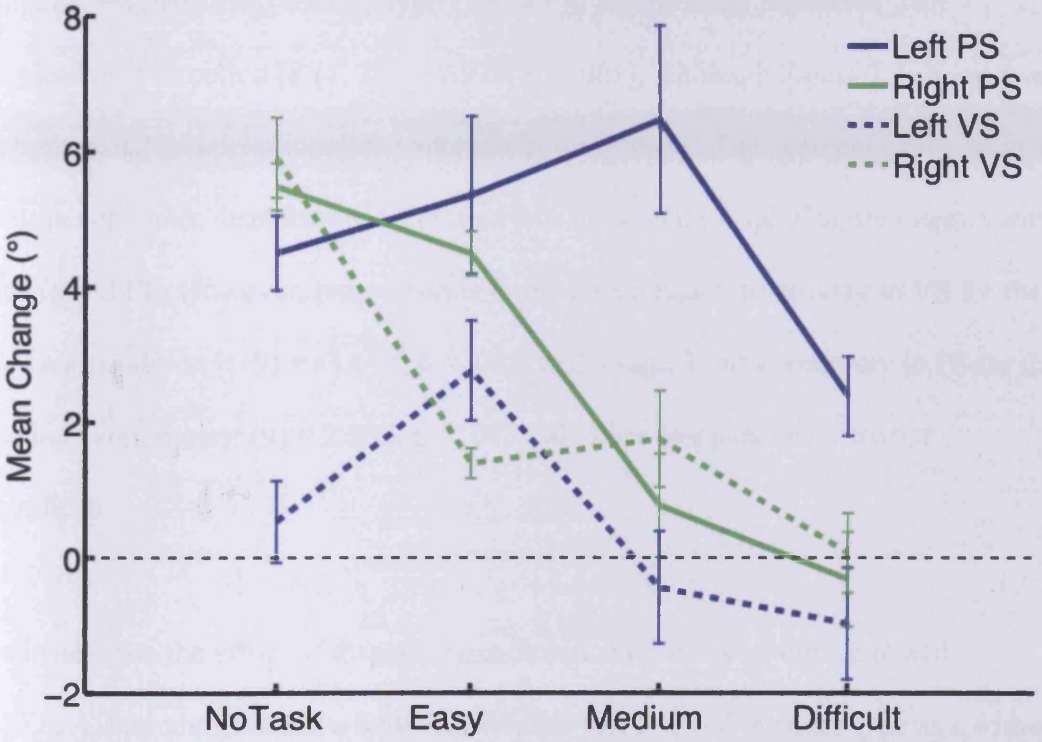

Figure 7.2. Differences in the magnitude of proprioceptive (PS) and visual (VS) adaptation for left and right displacements are shown at each level of secondary task difficulty in the Attention experiment.

Visual inspection of Figure 7.2 reveals that both visual and proprioceptive adaptation appear to be of similar magnitudes after rightward displacement exposure (green lines), whereas proprioceptive adaptation appears to be larger than visual adaptation after leftward displacement exposure (blue lines). Interestingly the effect of cognitive load appears to be more prominent during rightward displacement exposure; for leftward displacement exposure, most adaptation is found in the Easy condition and not the NoTask condition. Asymmetries in the magnitude of PS only seem to occur when participants were conducting the medium and difficult tasks, whereas asymmetries in VS are only present in the NoTask condition.

Reanalysis of the results, adding displacement direction as a further between subjects variable, revealed that measure type (VS or PS) significantly interacted with displacement direction [F (1, 72) = 7.971, p = .006]. Although Figure 7.3 shows a dip in both visual and proprioceptive adaptation for leftward displacement exposure in the Notask condition, displacement direction was not found to significantly interact with task (p = .119). However, paired t-tests found a significant asymmetry in VS for the NoTask condition [t (9) = -3.640, p = .005] and a significant asymmetry in PS for the Medium condition [t (9) = 2.352, p = .043], all other comparisons were not significant.

To investigate the effect of displacement direction on measure type, a mixed ANOVA, including task as a between subjects variable and measure type as a within subjects variable, was conducted on the data for left and rightward displacements separately. With regards to leftward displacement exposure, proprioceptive adaptation was found to be significantly larger than visual adaptation [F (1, 36) = 14.887, p <

.001], yet adaptation magnitude was not found to differ across secondary task difficulty (p = .392). In contrast, the results of the analysis of adaptation data for rightward displacement exposure revealed a significant effect of task [F (3, 36) = 10.946, p < .001], but a non-significant effect of measure (p = .701). This effect is presented clearly in Figure 7.2.

To sum up, displacement direction was found to significantly interact with the type of adaptation measured. Statistical analysis revealed that only exposure to a leftward displacement produced significantly more proprioceptive adaptation than visual adaptation. Displacement direction was not found to have a significant effect on task. Although the effect of cognitive load was only significant during rightward displacement exposure, this was likely to be driven by a significant asymmetry in the magnitude of VS in the NoTask condition. Interestingly, the original study conducted by Redding and Wallace (1985a), that also found an effect of cognitive load, only included exposure to a rightward displacement. However, Redding and Wallace (1985a) were also able to find a significant difference between the magnitude of VS and PS after rightward displacement exposure (p < .001), a finding that we were unable to replicate here.

The effect of exposure duration and exposure to optic flow

The combined results for the Timecourse experiment presented in Chapter 5 suggested that the timecourse of visual and proprioceptive adaptation differed as a function of time and exposure to optic flow: visual adaptation occurred much faster in the presence of optic flow, whereas proprioceptive adaptation occurred much faster in the absence of optic flow. Figure 7.3 shows the influence of displacement direction on these effects. Results are shown as a function of exposure to optic flow and exposure duration.

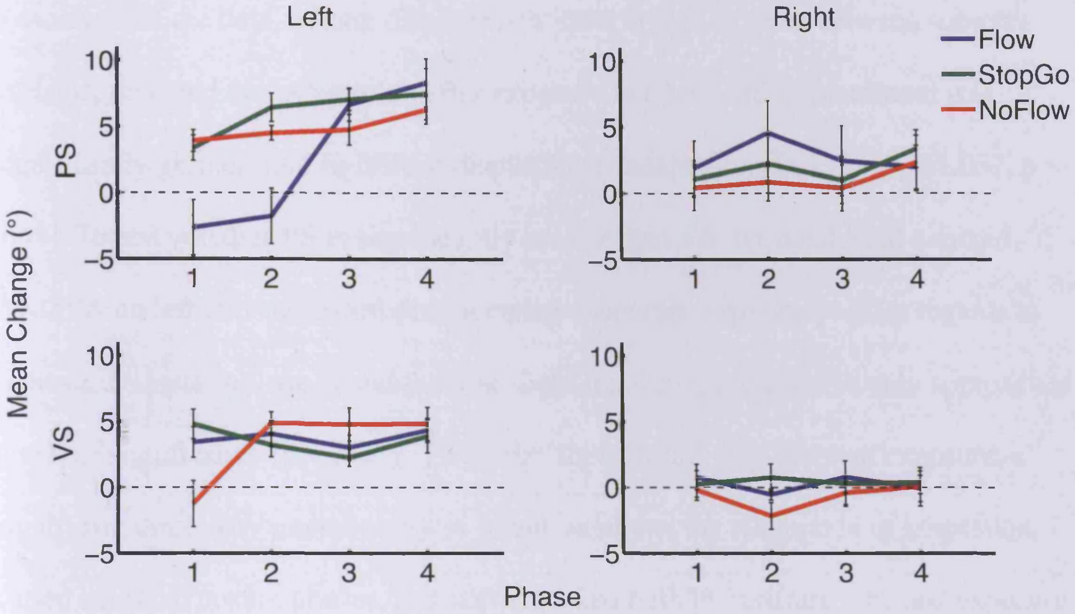

Figure 7.3. Mean perceived direction is shown as a function of exposure phase and optic flow exposure (Flow, StopGo and Noflow). The top two graphs show changes in perceived proprioceptive straight ahead; the bottom two show changes in visual straight ahead. Graphs on the left of the figure show recalibration while exposed to a leftward displacement, while those on the right show recalibration while exposed to a rightward displacement.

As can be seen in Figure 7.3, similar to the results of the Attention experiment, exposure to a leftward displacement appears to produce substantially more proprioceptive adaptation than rightward displacement exposure. Interestingly, visual adaptation also appears to be greater after leftward displacement exposure. When comparing the magnitude of PS and VS for each displacement direction, PS is larger than VS for both displacements; however, this trend is less apparent after rightward displacement exposure. Varying the availability of optic flow only seems to have an effect on adaptation to a leftward displacement.

Reanalysis of the data, adding displacement direction as an extra between subjects variable, revealed that adaptation after exposure to a leftward displacement was significantly greater than rightward displacement adaptation [F (1, 54), = 31.057, p < .001]. To test whether PS is significantly greater than VS, we conducted a mixed ANOVA on left and rightward displacement adaptation separately. With regards to rightward adaptation, we found that the slight trend suggested above only approached levels of significance (p = .091). However, for leftward displacement exposure, a significant three-way interaction was found, such that the magnitude of adaptation varied across exposure phases, and was modified both by measure type and exposure to optic flow [F (6, 81) = 7.667, p < .001].

In sum, the results of the asymmetries analysis for the Timecourse experiment revealed that, similar to the results for experiment 1 and 2 (NoFlow and FOV) the magnitude of adaptation was greater after exposure to a leftward displacement. Exposure to optic flow only affected recalibration when an observer was exposed to a leftward displacement. Interestingly, this contrasts with the results for the Attention experiment, which revealed that the introduction of a secondary cognitive task had a greater effect on adaptation to a rightward displacement.

PART 2: Asymmetries in heading error

Chapter 6 highlighted that a change in perceived visual direction could be mapped onto a change in heading error. In this sense one would intuitively expect the asymmetries in aftereffect measures demonstrated for the Timecourse experiment in Part 1 to be reflected in the heading error data. Figure 7.4 shows the mean target-heading error of each trajectory for all three optic flow conditions.

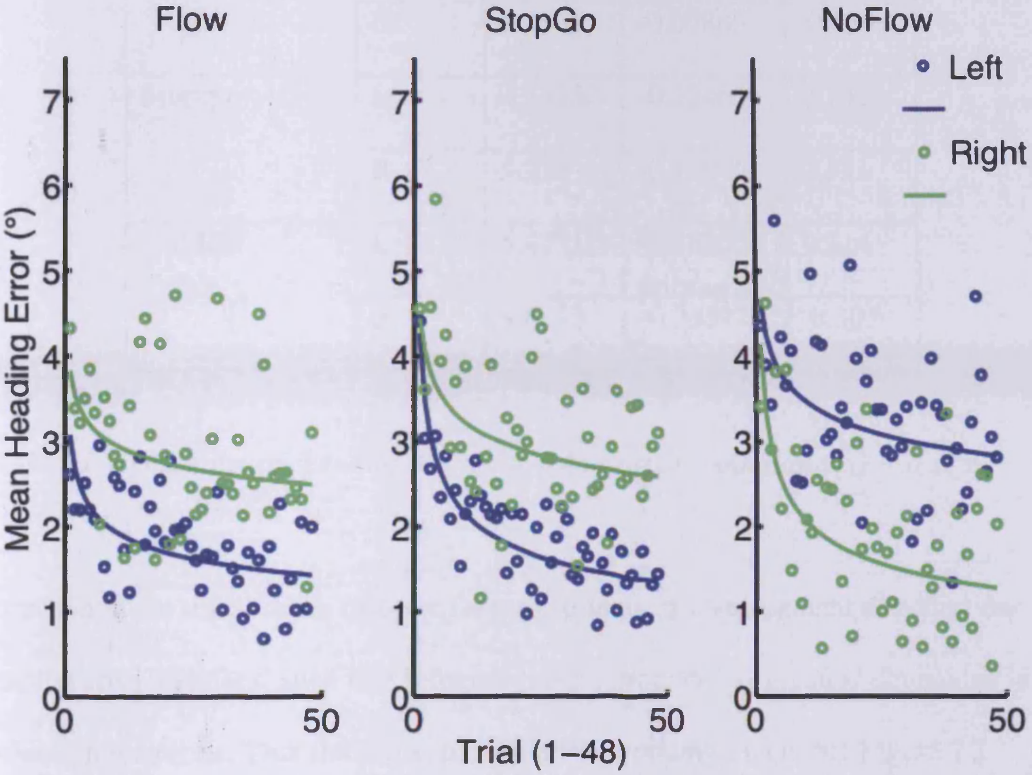

Figure 7.4. The effect of displacement direction on heading error across trials as a function of the availability of optic flow.

From the recalibration asymmetry presented for the Timecourse experiment (Figure 7.3), the change in perceived straight ahead was found to be larger after exposure to leftward displacing prisms. It could thus be predicted that the change in target-heading error would be largest while exposed to prisms that produce the *least* adaptation (rightward displacing prisms). Indeed this appears to be the case for the Flow and StopGo conditions: heading error is larger when exposed to a rightward displacement. Indeed, there appears to be little change in heading error across trials while exposed to a rightward displacement, particularly in the Flow condition, as reflected in the low R^2 value shown in Table 7.1.

Condition	Prism	a	n	R^2
Flow	L	3.2452	-0.13898	0.323
	R	4.4565	-0.07885	0.083
Stopgo	L	4.5035	-0.23465	0.703
	R	5.273	-0.13976	0.331
NoFlow	L	5.4781	-0.10857	0.214
	R	4.6853	-0.23517	0.305

Table 7.1. Evaluation of the data in Figure 7.4 using the equation y(x) = a x\^n

Interestingly, in the absence of optic flow the effects of displacement direction on heading error switches, such that leftward prisms produce the greatest deviations in walking trajectories. This finding is particularly surprising given that Figure 7.3 highlights that the magnitude of recalibration across all conditions is greater while exposed to a leftward displacement.

Relationship between changes in heading error and perceived straight ahead as a function of displacement direction

In Chapter 6 we established that the degree of change in perceived visual direction was comparable with the degree of change in heading error measured against baseline. Here we conducted the same analysis, partialing out displacement direction. Since the presence of optic flow is likely to produce a fast acting change in first trial heading error, we used the first trial of the NoFlow as our baseline. Rather than using a single data point, we used the intercept of the line fit for trials 1-6 (phase 1) as the best estimate of initial heading without any adaptation. As in Chapter 6, to estimate heading error on the last trial of a phase we bracketed the measures of perceived straight ahead by taking the mean of the heading error on the two trajectories proceeding the VS and PS measures, and the two trajectories immediately after. Figure 7.5 shows the outcome of the comparison between change in heading error and change in perceived straight ahead, for left and rightward displacements separately.

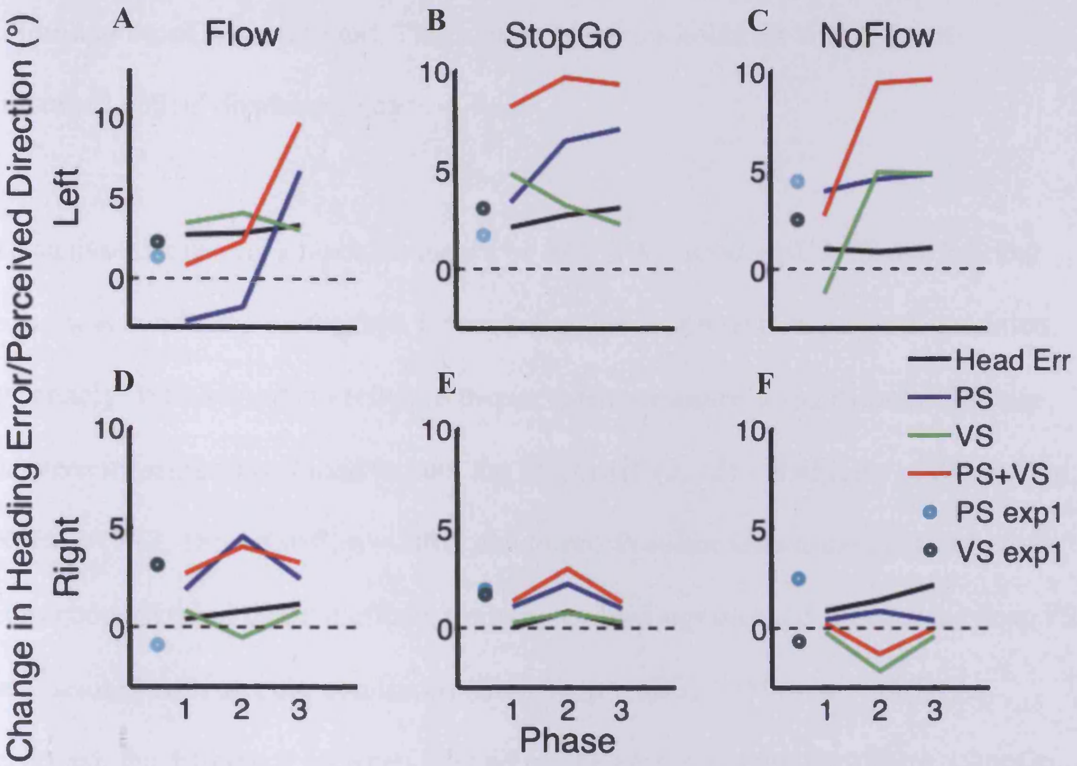

Figure 7.5. Change in heading error in degrees from the first of the NoFlow trials (best estimate of heading error without any adaptation) to the last trial for phases 1, 2 and 3 (bracketed trials 5-8; 11-14; 23-26 respectively). To represent heading error on the last trial of a phase, the mean of the last two trials and the first two trials of the subsequent phase was taken to overcome the potentially disruptive effects of measuring perceived straight ahead. Mean change in perceived direction (visual, proprioceptive and total – PS+VS) from pre- to post-exposure is displayed for comparison. PS and VS are also shown from experiment 1 (PS in cyan and VS in dark green). The top row corresponds to heading error and perceived straight ahead data for leftward displacement exposure; the bottom row shows rightward displacement data.

As demonstrated in Figure 6.5 of Chapter 6, change in visual straight ahead provides the best estimation of change in heading error, at least in the presence of optic flow

(Flow and StopGo conditions). This pattern of results holds for both left and rightward optical displacements.

To analyse the results a repeated measures ANOVA, including VS, PS and heading error, was conducted on the data for each displacement direction and each condition separately. With regards to leftward displacement exposure, a significant difference between measures was found in both the StopGo [F (2, 18) = 8.451, p = .003] and the NoFlow [F (2, 18) = 8.897, p = .002] condition. Post-hoc tests using the Bonferroni correction revealed that the effects were driven by a significant difference between PS and heading error in both conditions (StopGo, p = .013; NoFlow, p = .007). As expected, the difference between VS and heading error was not significant (StopGo, p = .507; NoFlow, p = .128). The latter, however, did approach significance. This is illustrated in Figure 7.5 C whereby VS is similar to heading error on phase 1, but not on phase 2 and 3. Indeed, paired t-tests found that VS was significantly different to heading error on phase 2 and 3 (p = .013; p = .003). In contrast PS was significantly different across all phases (p = .015; p = .001 p = .024)

Surprisingly, a repeated measures ANOVA found a non-significant effect of measure in the Flow condition (p = .177); however, there was a significant effect of phase [F (2, 18) = 9.488, p = .002]. This effect was driven by a change in PS: using paired t-tests, VS was not significantly different to heading error across all three phases (p = .451; p = .170; p = .947 respectively), in contrast, the difference between PS and heading error was only non-significant in phase 2 (p = .036; p = .066; p = .032 respectively)

With regards to the relationship between perceived direction and heading error while exposed to a rightward displacement, measure was not found to be a significant source of variance in all three conditions (Flow, p = .565; StopGo, p = .735; NoFlow, p = .237). This is likely to be consequence of the small changes found in all three measures.

The comparable data from experiment 1 (NoFlow experiment) are also plotted on the figure at phase 1. Although direct comparisons between experiment 1 and the Timecourse experiment are problematic due to the different designs used, the trend in the data at phase 1 of the Timecourse experiment is similar to that found for experiment 1 for both left and rightward displacements.

Target-heading error conclusions

To conclude, with regards to asymmetries in the mean heading error across trials, heading error is larger while exposed to rightward displacing prisms, as reflected in the smaller magnitude of change in perceived direction. This data is in line with the asymmetries found in adaptation: namely that the magnitude of adaptation in the Timecourse experiment is smaller after exposure to a rightward displacement. In contrast heading error is much less, and change in perceived straight ahead much larger while exposed to a leftward displacement. However, these trends are only consistent when optic flow is present. In the absence of optic flow we find a curious flip in the magnitude of heading error, yet the asymmetry in perceived direction remains the same.

Similar to the results presented in Chapter 6 we find that a change in visual straight ahead best represents the change in target-heading error, both when exposed to a leftward and rightward displacement. However, similar to the analysis of heading error across time we find that this relationship only holds in conditions when optic flow is present; when optic flow is absent it could be argued that change in proprioceptive straight ahead provides a better indication of change in target-heading error, particularly while exposed to a rightward displacement.

Summary and Discussion

The aim of this chapter was to investigate whether an asymmetry existed in the magnitude of adaptation obtained after exposure to left or rightward displacing prisms. The reviewed literature suggests that 'cognitive' aftereffect tasks, such as the line bisection task used by Colent et al. (2000), and the locomotor task of Michel et al. (2008), reveal significantly more adaptation to a leftward optical displacement. If measuring perceived straight ahead involves a cognitive element, then we should find more adaptation after exposure to a leftward displacement.

The general trend presented above was that exposure to leftward prisms produced a greater amount of both proprioceptive and visual recalibration. Although this relationship was not found to be significant in experiments that included shorter exposure times (experiments 1-3), the asymmetry found in the Timecourse experiment was significant. This pattern of data was also reflected in heading error: heading error while exposed to a rightward displacement was much larger suggesting less adaptation. Interestingly, this relationship was only found for the two conditions that contained optic flow. When optic flow was absent we found that recalibration was greater after a leftward displacement exposure; yet heading error was largest after exposure to a leftward displacement. Similarly, when comparing a change in perceived straight ahead with a change in heading error, we found that a change in visual straight ahead best accounted for a change in heading error, for both displacement directions, but only when optic flow was available.

The results of the Attention experiment demonstrated a different pattern of results: although PS was found to be significantly larger than VS only after leftward displacement exposure, unlike the effect of exposure to optic flow, the effect of cognitive load was more prominent during rightward displacement exposure. Since the optical devices used were both of high quality, made within the same laboratory, and produced a displacement of the same degree (but in opposite directions), it is unlikely that any differences in adaptation can be attributed to discrepant artefacts related to the prism glasses themselves.

Speculations with regards to the asymmetries

Above we have discussed research concerning adaptation asymmetry in healthy participants; asymmetries have also been found in patients with visual neglect (e.g. Rossetti, Rode, Pisella, Farne, Bosson & Perenin, 1998). Patients with neglect have an inherent bias towards the ipsilesional side of space, often failing to respond to the side of space opposite to their brain lesion (Danckert & Ferber, 2006). In contrast to the findings of Colent et al. (2000), Rossetti et al. (1998) demonstrated that, using a similar bisection task, aftereffects in patients with neglect were only found after exposure to *rightward* displacing prisms. Colent et al. (2000) suggested that this asymmetry might be linked to differences in the over-representation of a particular hemispace in the two groups: it is well known that patients with neglect have an inherent bias towards the side of space ipsilateral to their brain lesion (usually a bias to the right side of space, and a neglect of the left side, after right parietal damage; e.g. Halligan & Marshall, 1991). There is also some evidence to suggest that healthy individuals exhibit a small bias to the left, a phenomenon known as pseudo-neglect (Bowers & Heilman, 1980). Heilman and Van Den Abell (1980) suggested that pseudo-neglect is a result of an asymmetric representation of visual space: that is, in healthy individuals the left side of space is controlled predominantly by the right hemisphere, whereas the right side of space is controlled both by the left and the right hemisphere.

These differences may account for the asymmetry in adaptation found between patients with neglect and healthy controls: namely that, using certain 'cognitive' aftereffect tasks, recalibration is greater after exposure to leftward prisms in normal participants, due to right hemisphere dominance. In contrast, exposure to a rightward displacement produces greater adaptation in patients with neglect due to right hemisphere damage. This effect is only found in patients with neglect using certain cognitive tasks: tasks that involve perceptual judgments generally do not find significant aftereffects, whereas those using manual judgements do (e.g. Striemer & Danckert, 2010a). However, the precise nature of this interaction is yet to be defined (Striemer & Danckert, 2010b)

If one were to go with the hypothesis of Michel et al. (2008) then it could be suggested that the measures of perceived direction used in this experiment involved some form of behaviour that is predominantly controlled by the right hemisphere. However, the asymmetry in adaptation found in the Attention experiment does not fit with this conclusion. Michel (2006) suggested that exposure to a leftward displacement improves plasticity in the left hemisphere; perhaps a cognitive task impedes this process. Indeed, there is some evidence to suggest that counting is predominantly processed in the left hemisphere (e.g. Semenza et al., 2006). Nevertheless, although this effect is intriguing, we are unable to make any firm conclusions based on the results of our experiment.

Conclusions

The analysis provides new insights into adaptation of perceived visual and proprioceptive straight ahead. The finding that visual adaptation can be mapped onto a change in heading error for both displacement directions strengthens the argument put forward in Chapter 6, and is particularly important for those studying locomotion. The left/right asymmetries may also help to explain some disagreements within the literature, highlighting that it is important to look at the direction of displacement used in studies of recalibration.

Chapter 8: Egocentric direction in the visual guidance of walking in patients with visual neglect

Evidence presented in Chapter 6 supports the hypothesis that walking is guided by aligning the locomotor axis with the perceived visual direction of a goal. When perceived direction is biased through the use of prism glasses, locomotor trajectories are affected accordingly: rather than taking a direct path to a designated target, observers take a curved path in the form of an equiangular spiral. The curved trajectory is the result of the observer making corrective body movements in an attempt to realign the centre of their torso with the target.

Unilateral visual neglect (UVN) is a variable disorder characterised by a failure to attend to, or respond to, objects contralateral (opposite) to the side of brain insult; patients behave as if one half of their world no longer exists (Mesulam, 1981). This common clinical disorder often occurs after lesions to the right hemisphere – although patients with left brain damage may also show signs of contralateral, right-sided neglect at an early stage, this is more unusual and is often less severe (Beis, et al., 2004). Rushton et al. (1998) suggested that reports of walking trajectories of patients with UVN might be explained by a bias in perceived straight ahead (see Heilman, Bowers & Watson, 1983). Inspection of Huitema, Brouwer, Hof, Dekker, Mulder and Postema's (2006) data on the curved trajectories of patients with UVN shows a pattern that mirrors that produced by healthy observers wearing prisms. In this chapter, I investigate whether prisms can be used to null the bias in perceived straight ahead, and, in turn, impact on the walking trajectories of patients with UVN.

The most common reports concerning the lateral deviation in walking trajectories exhibited by patients with UVN involve bumping into objects, and people, in the neglected field, and in attempting to pass between doorframes (Verlander et al., 2000). One explanation for these trajectories relates to a misperception of direction, such that, similar to healthy controls, UVN patients attempt to realign their torso with the misperceived target location. Research looking at perceived direction in patients with UVN has clearly demonstrated a shift in perceived direction: for example, Heilman et al. (1983) reported that when patients with left UVN were asked to point straight ahead, perception of direction was shifted to the right side of space. Similarly, Ferber and Karnath (1999) described comparable results after asking patients to make a visual estimate of straight ahead by adjusting the position of an LED. It thus seems plausible to assume that the curved walking trajectories are related to a misperception of direction in UVN patients.

The literature relating to the walking paths taken by UVN patients is contradictory. Some researchers have found evidence suggesting that patients curve to the right of straight ahead (Robertson, Tegner, Godrich, & Wilson, 1994; Berti et al., 2002), whereas others have found that patients curve to the left while walking (Grossi, Lepore, Napolitano, & Trojano, 2001; Turnbull, & McGeorge, 1998).

The egocentric direction theory predicts that a patient whose perception of direction is endogenously shifted either to the left or right, should curve towards the side of space opposite to their bias in perceived direction (see Figure 8.1). For example, if straight ahead is perceived to be to the right, a target located veridically straight ahead will be perceived to be to the left. As a result of the misperceived target location, when asked to walk towards the target, the patient should take a curved trajectory to the left. We have already demonstrated that prisms can be used to bias perceived direction, in turn affecting locomotor trajectories in healthy individuals. It should thus be possible to use prisms to 'push' UVN patients' perception of direction back to its true position (Rossi, Kheyfets & Reding, 1990), in turn straightening locomotor trajectories (see Figure 8.1).

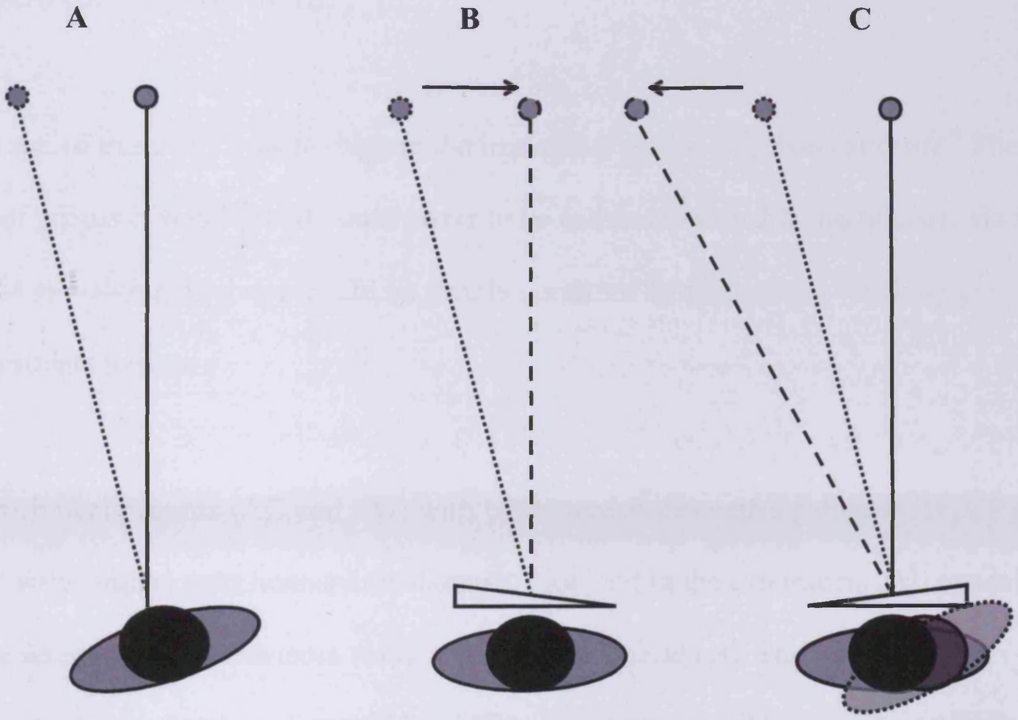

Figure 8.1. Schematic to illustrate how prisms can be used to change perceived target position in patients whose perception of straight ahead is biased to the right. The opposite result is expected in patients whose perception of straight ahead is biased to the left.

A: Due to the rightward bias in perceived straight ahead a target positioned veridically straight ahead is perceived to be to the left. To face the target the patient will turn to the left, producing a leftward curving trajectory en-route to the target.

B: Base left, rightward displacing prisms shift the perceived position of the target to the right. The target now coincides with perceived straight ahead. The patient should walk straight to the target.

C: Base right, leftward displacing prisms shift perceived target position further leftwards. The participant must rotate further to the left to align their torso with the perceived target position. This should result in a trajectory that deviates even further leftward (as compared to A).

The aim of this study was to explore the immediate effects of prism exposure.[6] The use of prisms in this context could prove to be extremely valuable, particularly since errors in walking direction could be simply corrected by prescribing 'walking glasses' for patients to wear.

Two clinical patients (AC and KO) with UVN, and three control patients (JW, CP and ML) with similar right hemisphere damage, took part in the experiment. All patients were screened for hemianopia using a simple visual field test. The individual characteristics of each patient will be outlined in greater detail below. The walking trajectories of all 5 patients were recorded in four conditions: (1) without prisms, (2) with rightward displacing prisms, (3) with leftward displacing prisms, and (4) without

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[6] Several researchers have already investigated the use of prism *adaptation,* (e.g. Rosetti Rode, Pissella, Farne, Li, Boisson, & Perenin, 1998) as opposed to on line prism use (e.g. Rossi et al 1990), to help with some of the functional problems associated with neglect. In their seminal paper, Rossetti et al (1998) highlighted that a small period of exposure to a rightward displacement was sufficient to produce a dramatic and comparatively lasting shift in performance on standard neuropsychological tests. Although the research discussed in this chapter is not concerned with the *aftereffects* of prism adaptation, as demonstrated by Rossetti and colleagues, we still took a measure of change in perceived direction from pre-to post-exposure.

prisms while conducting a secondary task. The predictions were in keeping with those of the egocentric direction theory discussed above: namely that prisms can be used directly to either neutralise or worsen the bias in perceived straight ahead associated with neglect, and in turn, straighten or worsen walking paths accordingly.

Methods

The experiment was conducted across two test sessions, seven days apart. There were four walking conditions, and participants took part in two conditions in each test session. Two of the walking trials required the patients to wear 9° prism glasses – one pair base left (rightward displacing prisms), and one pair base right (leftward displacing prisms). These were the same glasses as those used in the previous experiments with healthy observers. All walking trials were conducted in a quiet hospital corridor (approximately 2.5m wide), except for control patient CP whose walking trials took place in a small recreation room adjacent to the hospital.

Participants were asked to walk back and forth between two targets (the experimenter and an assistant) with the aim of "high-fiving" the target (experimenter) when they reached it (the experimenter held up the palm of their right hand, and the patient was required to hit it when they reached the experimenter). Upon reaching the target, participants were asked to turn around, fixate on the target at the opposite side (from where they had just walked), and walk towards it. The distance between the targets was 8 metres, and participants were required to walk between them eight times (or as many as permitted by their walking ability), resulting in a total of sixteen trajectories.

All patients were able to complete all sixteen trajectories, in all four walking conditions.

To record the walking trajectories, two Sony camcorders were set up at either end of the walking area in front of the targets. The cameras were attached to a tripod at a height of 70cm from the ground, and were positioned on an angle of approximately 45° downwards so that the base of the tripod holding the other camera, at the second target location, was at the top of the image in the viewfinder. The cameras were positioned in this way to meet ethical requirements; since only their footsteps were recorded, participants remained anonymous in the video footage. Video footage was analysed using Adobe After Effects. To enable this analysis, prior to the commencement of each experimental session, the position of the cameras and distance of the walkway was calibrated: the experimenter would place a metre ruler at 1 metre intervals perpendicular to a tape measure run between the two cameras. This enabled x, y coordinates to be extracted to aid subsequent video analysis. The tape measure and ruler were removed during the experimental trials.

We attempted to measure both proprioceptive and visual straight ahead (we were only able to measure proprioceptive straight ahead in three out of the five patients). Perceived straight ahead was measured in the standard way as described in Chapter 2: for visual straight ahead the patient was asked to sit two metres from a straight wall while the experimenter moved a laser pointer slowly across the surface, starting randomly either from the right or from the left. Participants had to verbally indicate when they perceived the pointer to be straight ahead, the experimenter could then read the point at which the participant indicated straight ahead to be off a small ruler placed on the wall. This procedure was repeated four times prior to, and after exposure to the prisms. To measure proprioceptive straight ahead, the patient sat in the same position and was asked to point straight ahead with a laser pointer while their eyes were closed.

The presence of UVN was assessed using the collective six subtests of the Behavioural Inattention Test (BIT, Wilson, Cockburn & Halligan, 1987): line cancellation, letter cancellation, star cancellation, figure copying, line bisection and representational drawing. The cut-off score for normality is 130/146. The BIT assessment tool is a standardised form of evaluation that measures everyday skills related to UVN, and provides an accurate description of a patient's strengths and weaknesses.

<u>Session 1:</u> After initial assessment of UVN (using the BIT) and perceived straight ahead (both visual and proprioceptive direction where possible), participants were required to conduct the first of the four walking conditions – normal walking, without prisms. As described above participants were asked to walk back and forth between two targets (experimenters) eight times as two camcorders recorded their footsteps. After completing the first sixteen trajectories, participants were given a short rest break before commencing with the second condition – walking while exposed to leftward displacing prisms. The walking procedure was the same as in the normal walking condition. At the end of the exposure session, participants completed a second assessment of perceived straight ahead. The second assessment of perceived direction was used to test if patients adapted to the prismatic displacement (i.e. if they experienced a change in perceived direction).

Session 2: Participants were given a seven-day break between session 1 and 2. Session 2 began by measuring observers perceived straight ahead and was followed by two conditions: (1) walking while exposed to base left, rightward displacing prisms, (2) walking normally while conducting a difficult secondary task (without prisms). The attentional manipulation was conducted to reveal any underlying deficits that might be compensated by the strategic use of conscious cognitive monitoring strategies. It was hypothesised that an attentionally demanding task would remove the cognitive resources necessary for monitoring walking direction. Perceived straight ahead was measured after exposure to the prisms while participants took a break between the two walking conditions. Participants were also tested again on the six subtests of the BIT to check for any changes on these neuropsychological tests.

Results

Control patients

Two right hemisphere stroke patients (one male – ML, and one female – JW), and one male patient (CP) who suffered similar right hemisphere damage after a severe encephalitis infection, were included as controls. All patients scored within the normal range on the BIT, and varied in age from 22 to 54. Patient JW was recruited from the Regional Stroke Unit at Cardiff Royal Infirmary (Cardiff and Vale University Health Board). Patient ML was an outpatient at Llwynypia Hospital (Cwm Taf NHS Trust), and patient CP was an outpatient at Rookwood Hospital (also part of the Cardiff and Vale University Health Board). All patients were right handed and were able to walk independently unaided.

Perceived straight ahead

The results of measures of perceived straight ahead are presented in Figure 8.2. Data from the three control patients were combined since perceived straight ahead was similar across participants.

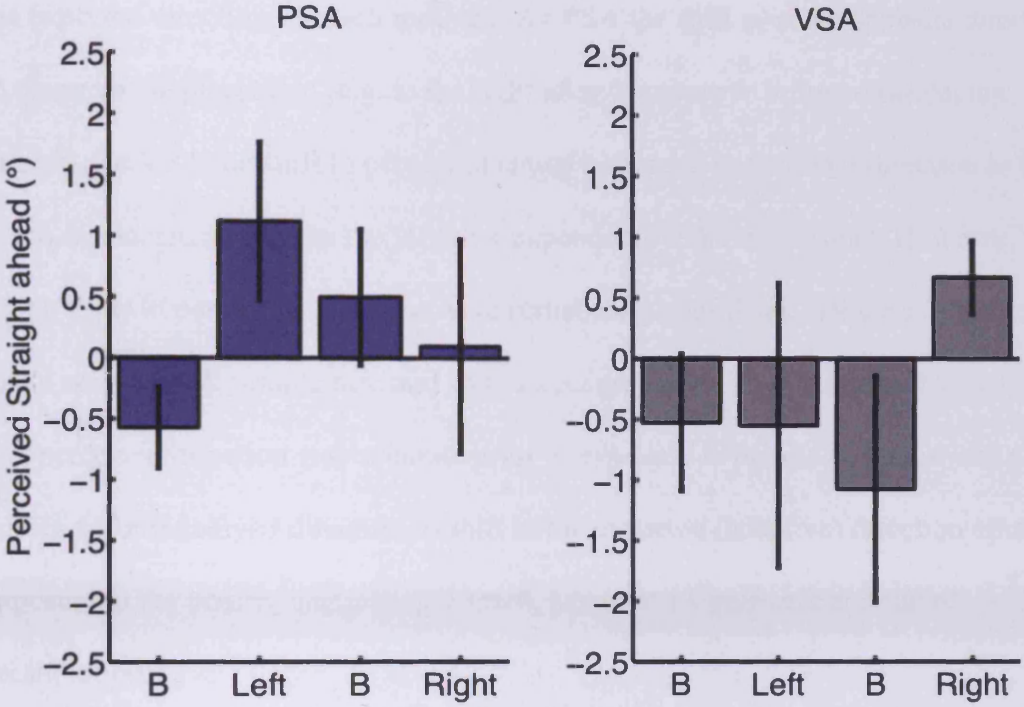

Figure 8.2. Estimates of perceived direction both before and after prism exposure. Mean estimates are shown for all three control patients. B =baseline measure of perceived straight ahead (taken prior to exposure to the prisms). Left/Right refer to perceived straight ahead after exposure to the prisms. PSA = proprioceptive straight ahead; VSA = visual straight ahead. A positive value indicates that perceived straight ahead is to the right of its true position, a negative value indicates that perceived direction is biased to the left. Error bars = ± 1 SE

Across both measures of perceived direction, there was a tendency for perceived straight ahead to be located to the left of its true position prior to exposure to the prisms (B – baseline measures). However, none of these biases were significantly different from zero (PSA: Left B p = .450; Right B p = .260. VSA: Left B p = .353, Right B p = .807).

The shift in perceived straight ahead after exposure to the prisms (while walking) is in the expected direction for each measure: for PSA the shift is in the opposite direction to the prism displacement (e.g. to the right after exposure to leftward displacing prisms), for VSA the shift in perceived straight ahead is in the same direction as the prism displacement (e.g. to the left after exposure to leftward prisms). However, none of the shifts in perceived direction were statistically significant. This was expected given such a small sample size and short exposure times. The main result to note is that perceived direction was accurate prior to exposure to prisms and there was a tendency for perceived direction to shift in the expected (adaptive) direction after exposure to the prisms, suggesting a small, albeit non-significant amount of recalibration.

Walking Trajectories

Mean walking trajectory across all 16 trajectories for each control patient is shown in Figure 8.3.

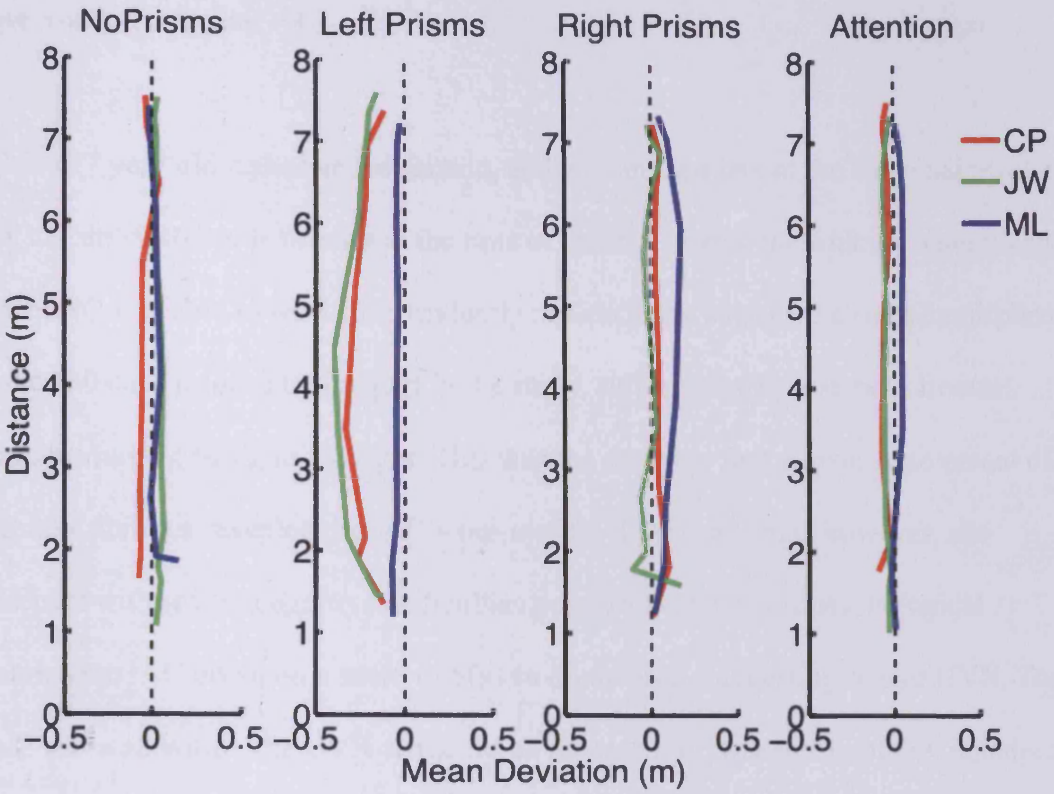

Figure 8.3. Mean walking paths for each of the three control patients in all four conditions. A deviation to the left is shown by a negative value, whereas a deviation to the right is shown by a positive value.

As expected, based on the accurate perception of perceived straight ahead shown in Figure 8.2, walking trajectories in the 'No Prisms' condition were reasonably straight – similar to what has been found before in right-hemisphere stroke patients without UVN (Huitema et al., 2006). Furthermore, similar to healthy controls, we found that prisms could be used to induce a curved trajectory according to the direction of the prismatic displacement. However, although each observer showed a change in walking trajectory as a function of prism exposure, each observer demonstrated an asymmetry (in line with the literature on prisms – Welch, 1978; Warren & Piatt, 1974), exhibiting a larger shift in one direction.

Case Study 1: Patient AC

AC is a 77 year-old right-handed female, and was an inpatient at the Regional Stroke Unit at Cardiff Royal Infirmary at the time of testing. During the walking assessment patient AC was able to walk independently unaided. She sustained a right-hemisphere stroke 130 days prior to taking part in the study, suffering infarcts in both frontal lobes, the largest being in the right. This was the patient's first stroke. Assessment of cognitive abilities revealed that AC's pre-morbid IQ was average; however, she presented with severe cognitive difficulties post-stroke. On neuropsychological examination, AC obtained a score of 50/146 on the BIT, suggesting severe UVN. This score was well within the UVN range for all six tests. AC was most notably impaired on the letter cancellation task crossing out only one of the required letters at the rightmost edge of the page. At the end of session 2, when given the BIT again, change in performance was minimal, and was not present for all BIT sub-tests, suggesting that the severity of her neglect remained consistent across time.

Perceived Straight-Ahead

Only perceived visual straight ahead could be measured in patient AC. Changes in perceived visual direction are displayed in Figure 8.4. It can be seen that prior to exposure to the prisms, visual straight ahead was perceived to be to the right (+1.7°). However, although this finding was in keeping with previous research, it was much less than might be expected; for example, Ferber and Karnath (1999) found a mean shift of 5.1° (SD 1.7°). After exposure to leftward displacing prisms while walking, perception of straight ahead shifted leftward as expected, suggesting adaptation– visual aftereffects occur in the same direction as the prismatic displacement (see

Chapter 2). However, changes in perceived visual straight ahead from pre- to post-exposure were not found to be significant for leftward displacing prisms (p = .387).

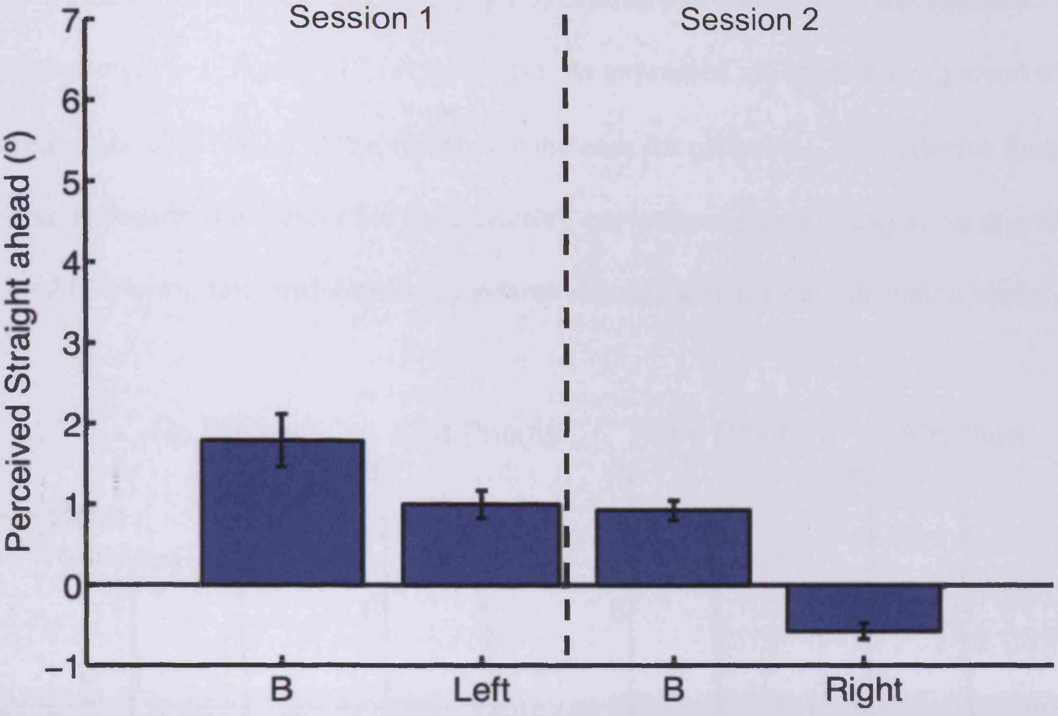

Figure 8.4. Mean location of perceived visual straight ahead prior to (B – baseline) and after exposure to each displacement direction (Left/Right). Positive numbers indicate a shift to the right of veridical straight ahead. Error Bars = ± 1 SE

For session 2 perception of straight ahead was slightly less biased prior to exposure to the prisms (0.86° difference). Unexpectedly, perceived visual straight ahead showed a significant shift further leftwards after exposure to the rightward displacement [t (3) = -3.392, p = .043]. This is a surprising finding given that visual adaptation is expected to occur in the same direction as the prismatic displacement – in this case to the right, but again highlights asymmetries in the effects of prisms.

Walking Trajectories

The data presented in Figure 8.5 corresponds to the mean trajectory across all 16 trials for each condition. The dotted blue line indicates the predicted trajectory based on AC's indication of visual direction prior to exposure to the leftward and rightward displacement (+1.7° and +1° respectively). As expressed in Figure 8.1, if perceived straight ahead is biased to the right (as is the case for patient AC), trajectories should curve leftwards. To correct for the trajectory curvature rightward displacing prisms should be worn; leftward displacing prisms should make the path deviation worse.

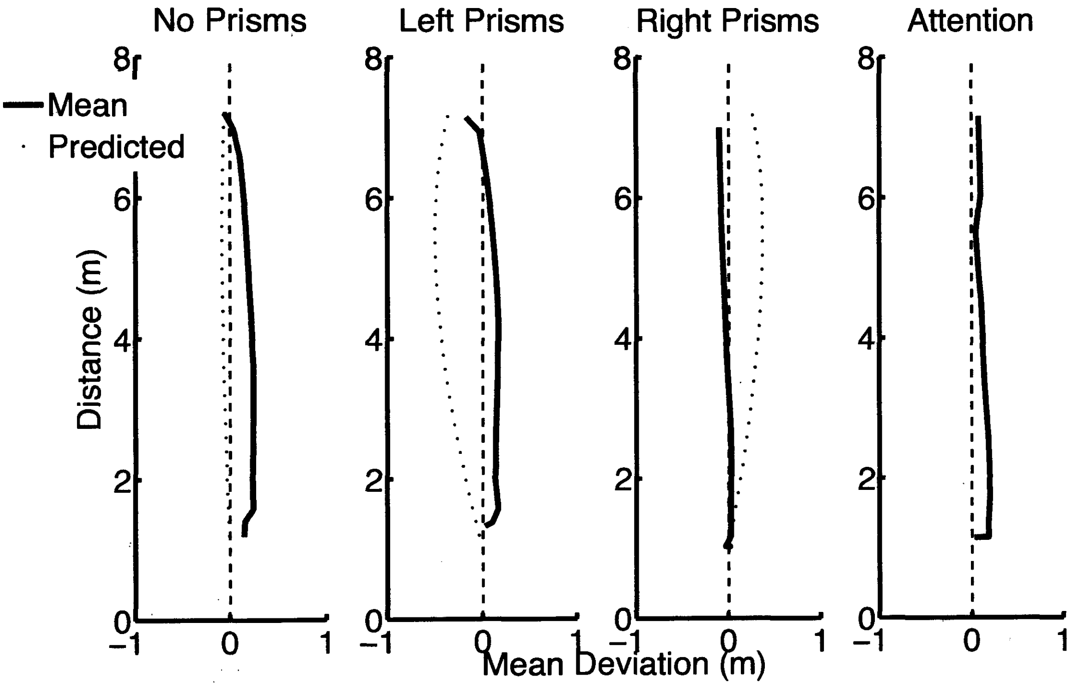

Figure 8.5. Plan view of the mean walking trajectories for all four walking conditions. The dashed black line indicates a straight walking trajectory. The dotted line in the No Prisms condition represents the predicted trajectory based on AC's perception of visual straight ahead. The predicted trajectory in the Prisms condition is based on AC's prior indication of perceived direction plus the 9° deflection of the prisms.

Figure 8.5 highlights that patient AC does not demonstrate a large deviation in her walking paths across all four conditions, and the deviations that do exist are much less than that expected according to the egocentric direction predictions. Although in Chapter 2 we established that the perceived deflection of the prisms was 7.5° within the confines of the outdoor environment used in the previous experiments, we were unable to take such measures within the environment used to measure patient trajectories. We thus based our trajectory predictions on the power of the prisms (9°). It is therefore unsurprising that the predicted trajectories presented in Figure 8.5 are much larger than patient AC's walking deviation. Furthermore, there is also evidence to suggest that patients can develop strategies to enable them to overcome the effects of UVN on their walking trajectories (e.g. the case of patient WV, Rushton et al., 1998). However, it is unlikely that patient AC was using a conscious correcting strategy since the attentionally demanding secondary task did not have an effect on her walking trajectories.

There are several aspects of the trajectory data worth noting: in the 'No Prisms' condition AC's walking trajectory deviated towards the right side of space – the opposite side expected based on her perception of visual straight ahead. However, it may well be the case that AC's walking direction reflects a misperception of proprioceptive straight ahead, an aspect of perceived direction that we were unable to measure. Indeed, as predicted, wearing rightward displacing prisms appeared to eliminate the deviation in walking trajectory. Leftward displacing prisms had no effect. With regards to the attentional manipulation, interestingly, cognitive load did not seem to have a detrimental impact on AC's walking behaviour. Possible reasons for this are discussed later.

Case study 2: Patient KO

KO is a 62 year-old right-handed male who was able to walk independently with the aid of a walking stick. At the time of testing he was an outpatient at the Regional Stroke Unit at Cardiff Royal Infirmary. Patient KO had no history of previous stroke before sustaining a right hemisphere stroke 183 days prior to taking part in the experiment. A CT scan showed a lesion in the right middle carotid artery. Neuropsychological testing revealed KO's pre-morbid IQ to be within the normal range. However, although his post stroke IQ was reduced patient KO's fluency and language skills remained within the normal range. Examined on the BIT, KO obtained a total score of 85/146. Although he performed within the expected range for UVN in five out of the six tests, he was 100% correct on the line cancellation subtest. At the end of the second session, when asked to complete the BIT again, performance remained similar.

Perceived Straight-Ahead

Similar to patient AC, we were only able to measure perceived visual direction in patient KO. Changes in perceived visual straight ahead as a function of displacement direction are displayed in Figure 8.6. Although KO presented less severe neglect, his perception of straight ahead was shifted 6.7° (4.91° further into the ipsilateral field than patient AC's). After exposure to a leftward displacement, the shift in perceived direction was found to be significantly further leftward [$t(3) = 4.531$, $p = .02$].

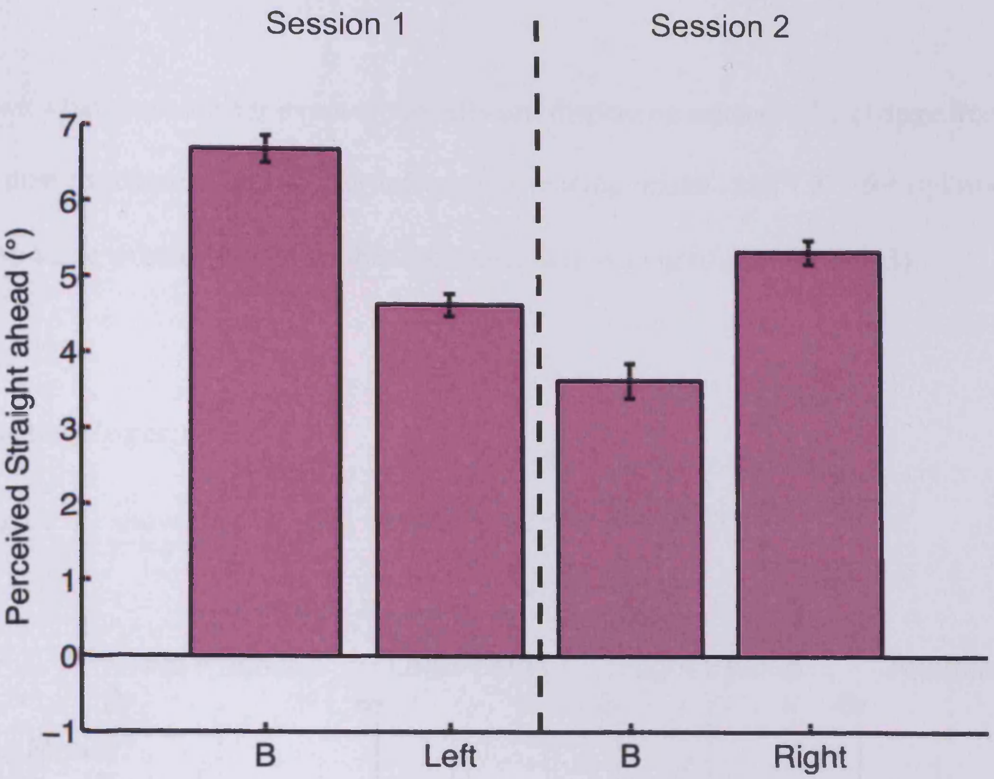

Figure 8.6. Mean perceived visual straight ahead is shown both prior to (B – baseline), and after exposure to a leftward (session 1) and rightward (session 2) displacement. Positive values indicate perceived direction is to the right of its true position. Error bars = ± 1SE

For session 2 KO's perception of visual straight ahead prior to exposure to the rightward displacement was substantially smaller than session 1 (by 3.05°). This may be due to the long lasting effect of adaptation to a leftward displacement in session 1. Indeed, research suggests that the effects of prisms can last for several weeks (e.g. Frassinetti, Angeli, Meneghello, Avanzi, & Ladavas, 2002). However, it is likely that the change is simply a reflection of drift. Unlike the aftereffect found for AC, exposure to the rightward displacement shifted KO's perception of visual straight ahead further to the right, in the adaptive direction as expected, and this aftereffect was found to be significant [t (3) = -4.071, p = .03]. The magnitude of adaptation was somewhat greater after exposure to leftward displacing prisms – the change from pre- to post-exposure was 2.06° for leftward displacing prisms, and 1.71° for rightward displacing prisms; however, this difference was not significant (p = .653).

Walking Trajectories

Figure 8.7 shows the walking trajectory data for patient KO.

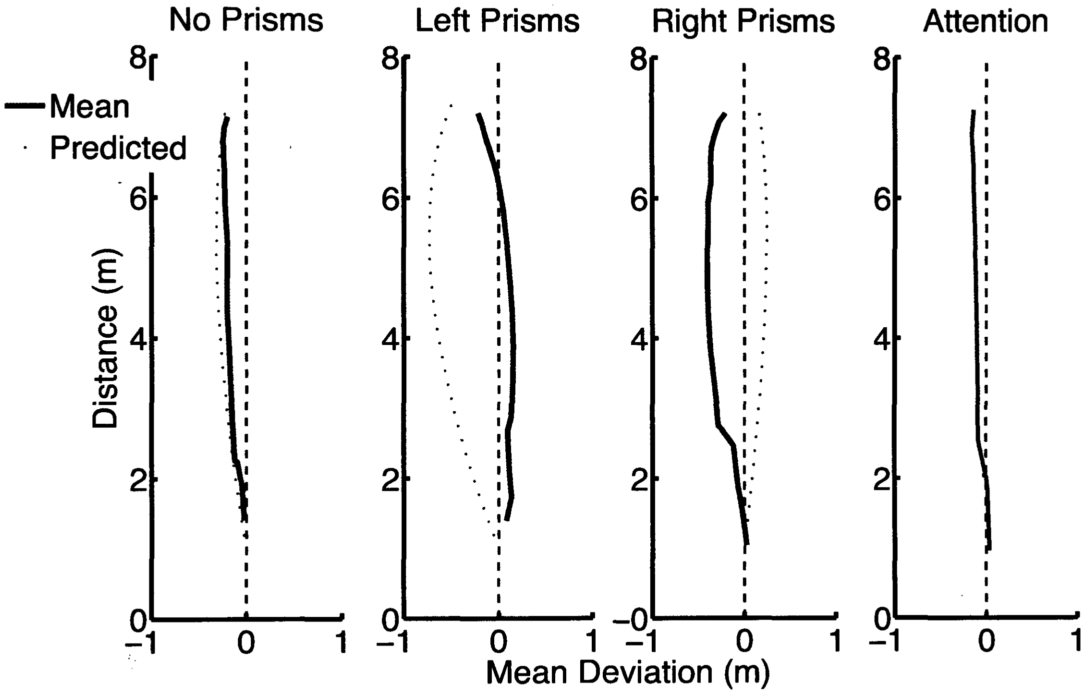

Figure 8.7 Plan view of the mean trajectory for each of the four walking conditions for patient KO. Egocentric direction predictions based on perceived visual direction are represented by the dotted line.

Starting with the 'No Prisms' condition Figure 8.7 illustrates that patient KO's walking trajectory deviated to the contralesional side of space, suggesting a misperception of direction to the right (as also highlighted in his walking direction).

Unlike what was found for patient AC, the magnitude of patient KO's trajectory deviation was very similar to what was expected according to his misperception of visual straight ahead (indicated by the dotted pink line). Exposure to leftward displacing prisms was expected to worsen KOs trajectories by pushing the perceived location of the target position further leftwards. However, leftward displacing prisms had the opposite effect to that expected: unlike what we found for patient AC, exposure to a leftward displacement appeared to improve KOs walking trajectories, and even shift them in the opposite direction. Rightward displacing prisms only served to increase the magnitude of the initial trajectory deviation. Interestingly, the addition of a secondary cognitive task did not worsen the deviation, as expected, similar to the results for AC it appears that the introduction of a secondary task did not cause a greater deviation in walking trajectory as compared to the No Prisms condition. Indeed, it appears that the counting task served to reduce the magnitude of the trajectory deviation.

When comparing across the two patients, it is clear that we have two very different sets of results: Patient AC's walking direction did not fit with her indication of visual straight ahead, yet, as predicted, we were able to correct her walking direction using rightward displacing prisms. Leftward displacing prisms had no effect. In contrast, patient KO's walking direction was in line with his biased perception of visual straight ahead. However, we were unable to correct for this deviation using rightward displacing prisms, indeed, exposure to a rightward displacement appeared to exacerbate his trajectory curvature. Leftward displacing prisms had the opposite effect, producing much straighter walking trajectories. Although measures of visual direction indeed revealed a rightward bias in straight ahead, the results of patient AC highlight that there is not a clear relationship between perceived visual direction and walking direction. It is indeed likely that perceived proprioceptive straight ahead could explain the bias in walking direction. However, since we were unable to measure proprioceptive straight ahead, no clear conclusions with regards to this can be drawn.

Summary and discussion

In Chapter 6 we demonstrated that when an error in perceived direction is artificially introduced through the use of prisms, heading direction is subsequently affected, such that a straight walking trajectory becomes curved. In this chapter, some control data was first presented to illustrate that, as in healthy controls, walking direction can (in neurological patients) be shifted to the left or right according to the direction of an induced bias in perceived straight ahead. In two case studies it was also demonstrated that when an inaccurate perception of direction has clinical roots, prisms could also be used to eliminate the error, in turn causing curved walking trajectories to become straighter.

Due to equipment restrictions it was not possible to collect estimates of proprioceptive straight ahead in the case study patients. As a result, the findings currently suggest that the prisms had the desired effect on walking direction for only one of our two case study patients: patient AC demonstrated a rightward bias in perceived straight ahead, and, as predicted, wearing rightward displacing prisms served to reduce the curvature in her walking paths. However, unlike what was predicted, prior to the introduction of prisms, AC's rightward bias in visual straight ahead did not produce a leftward deviating walking trajectory. In contrast, although patient KO's walking direction matched his perception of visual straight ahead, his walking direction could not be corrected for using a rightward displacement as predicted. Instead, KO's trajectories were corrected for using rightward displacing prisms.

The trajectory results thus highlight the importance of collecting data relating to both visual *and* proprioceptive direction. However, arguably a clinician may not need to collect measures of straight ahead, but instead could simply note the direction of the deviation and prescribe walking glasses to correct for this. Our results suggest a deviation to the left can be corrected using leftward displacing prisms, and a deviation to the right can be corrected for using rightward displacing prisms. However, as our results stand, they do not fit entirely with the principles of the egocentric direction model. It would therefore be interesting to collect data to see if proprioception mirrors the bias found for visual direction, or if the two measures of perceived direction are dissociated in patients with UVN. Indeed, as described in Chapter 2, although both forms of direction can be mapped onto a common reference frame – the trunk – they both rely on signals from different sensory systems. Thus, it may well be the case that the bias in walking direction presented above is a result of a misperception of proprioceptive direction.

Other authors have offered different explanations as to why differences in the direction of trajectory deviation might occur. Tromp, Dinkla and Mulder (1995) suggested that the difference in deviation direction found across patients in their experiment could be accounted for by the severity of UVN. Their results demonstrated that, not only did patients with more severe neglect have a higher collision rate when attempting to pass through an aperture; their collisions were more likely to be to the right side of space. Indeed, in our experiment, AC's neglect was more severe than patient KO's, and, similar to the 'severe' patients in Tromp et al. (1995), it was patient AC who deviated to the right side while walking. However, since Tromp et al. (1995) did not measure perceived direction, it is still possible that differences in perceived straight ahead caused the differences in walking direction found in their results. Indeed, it is possible that the severity of neglect could have a differential effect on perceived direction.

Huitema, et al., (2006) suggested that the differences in walking trajectory direction could be accounted for by examining the walking ability of the patient: that is, when walking ability is not severely impaired, patients should deviate to the neglected (left) side, as expected. Huitema et al. suggested that differences in the walking trajectories of patients in Tromp et al.'s (1995) experiment could be accounted for by differences in walking speed. Indeed, Huitema et al.'s results revealed that only patients whose walking ability was impaired veered to the right while walking. Although in our experiment walking ability was not quantified using standard tests, it was patient AC who was able to walk completely unaided, and so, according to Huitema et al., should deviate to the left. In contrast, patient KO walked with a stick and thus, according to Huitema et al., should deviate to the right, but this is not what we found. Using walking speed as an index of walking ability Figure 8.8 highlights differences across all four walking conditions for each case study patient.

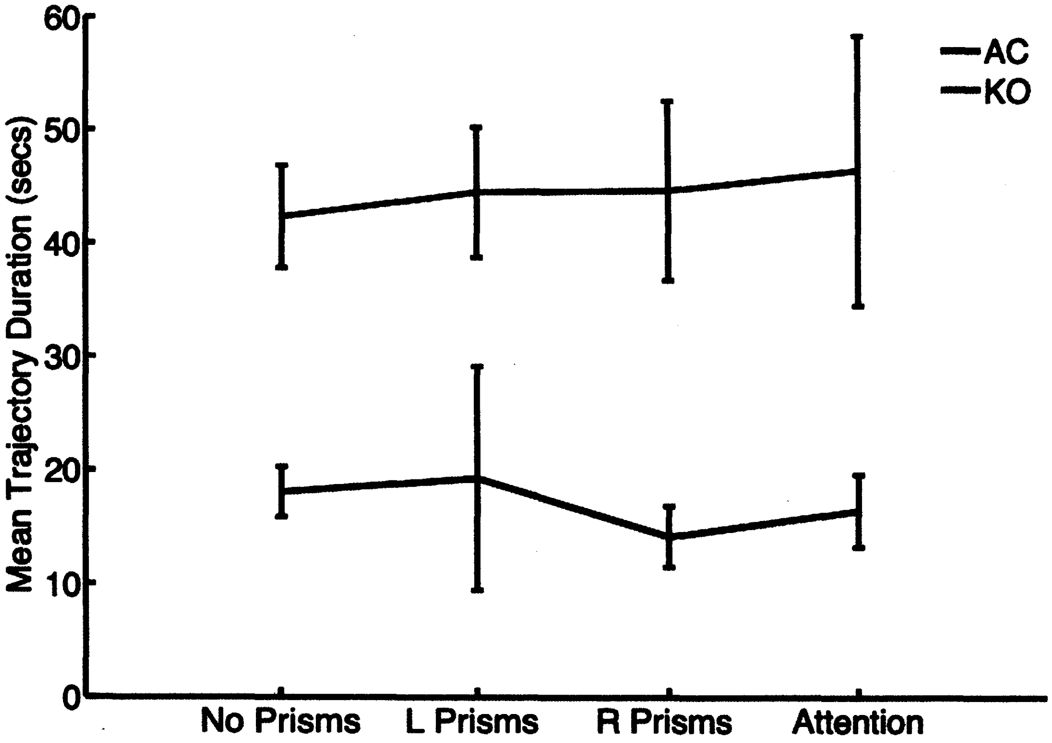

Figure 8.8. Mean trajectory duration for patient AC and patient KO across all four walking conditions. Mean trajectory duration is taken as an indication of walking speed. Error bars = ± 1SD

The interpretation of Huitema et al. (2006) does not hold for the results of this experiment since it was patient KO who had the slowest walking speed across all four conditions, yet it was patient AC whose walking trajectory deviated to the right. The behaviour is thus not a product of a locomotor dysfunction, secondary to the effects of stroke. The most parsimonious explanation for the difference in walking trajectory direction relates to a bias in perceived direction. Indeed, there is evidence to suggest that a bias in perceived egocentric direction can account for a deviation in walking direction found in patients with Parkinson's disease (PD): Davidsdottir, Wagenaar, and Young (2008) examined the relationship between perceived proprioceptive straight ahead and walking direction using two groups of patients with PD: those with initial symptoms to the left side of the body (inferred right hemisphere pathology), and those with initial symptoms to the right side of the body (inferred left hemisphere pathology). Although the deviation in perceived proprioceptive direction differed as a function of gender and group, there was a significant correlation between the deviation in perceived proprioceptive straight ahead and the direction of veering while walking. Unfortunately, Davidsdottir et al. (2008) did not measure visual straight ahead.

One final interesting finding from our study to note is that conducting a secondary cognitive task while walking appeared to have no effect on the walking trajectories of the case-study patients. If anything, conducting a secondary task made the walking trajectories straighter. This finding questions the functional task demands of the attentional manipulation, highlighting the possibility that the task was not as demanding as expected. Indeed, the duration of walking trajectories did not increase when patients were given a secondary task. However, while observing the patients it did appear that they struggled with the secondary task. Another possible explanation is that the secondary task served to increase arousal, and that this reduced the bias: for example, Robertson, Tegnér, Kham, Lo and Nimmo-Smith, (1995) found that increased activation of the attention system improved UVN.

In conclusion, the results from the two case study patients are both variable and indeed contradictory, and, given the small sample size and measurement limitations, the findings need to be interpreted with caution. Although others have suggested alternative explanations as to why the deviation in walking trajectory may vary across patients with UVN (Tromp et al., 1995; Huitema et al., 2006), these suggestions do not fit with our data, but neither can they be fully discounted. Furthermore, since these studies did not include a measure of perceived direction, the influence of a bias in straight ahead cannot be ruled out.

Although we were unable to uncover a simple relationship between perceived direction and walking direction in our sample, it should be noted that patient studies are notoriously difficult to conduct. A much larger sample is needed to make any firm conclusions; however, studies are limited by the fact that ambulatory neglect patients tend to be uncommon. To determine the link between perceived straight ahead, neglect and trajectory, our findings highlight the importance of including measures of both perceived proprioceptive direction and visual direction. Using both measures will provide a more complete account of perceived direction in a given patient. With regards to our data, although the conclusions, given the results and limitations, have inevitably to be speculative, they can be regarded as pilot studies that will inform future research.

General Discussion

Summary

In the previous chapters we presented several studies examining the role of optic flow in the recalibration of perceived direction. A number of methods were employed to shed light on different aspects of the recalibration process. Recalibration was measured by using two tasks that are known to be sensitive to change within two distinct sensorimotor systems (Redding & Wallace, 1997): the visual (eye-head) system, and the proprioceptive (hand-head) system.

Perceived direction was measured both prior to and after exposure to either left or rightward displacing prisms. In Chapter 2, we presented evidence to suggest that these measures would enable us to derive the best estimate of recalibration in perceived direction. We reviewed the relative advantages of prisms vs. other methods, and concluded that prisms provided the best means for perturbing perceived direction.

In Chapter 3, we examined the role of optic flow, and an error signal, in recalibration. We addressed these factors across three walking experiments: in experiment 1, we temporally manipulated exposure to optic flow so that it was continuous, intermittent, or not available. We found that the magnitude and site of adaptation varied as a function of exposure to optic flow: that is, when optic flow was continuously available, change in perceived direction was primarily visual; when optic flow was absent, recalibration occurred primarily within the proprioceptive system.

In a second experiment we spatially manipulated exposure to optic flow by restricting observers' field of view (FOV). In the unrestricted condition we found adaptation was primarily visual. However, the site of adaptation switched towards proprioception as vision became more restricted. Thus, in line with the results of experiment 1, we found that the site of adaptation varied with the availability of optic flow.

In a third experiment we specifically examined the role of an error signal in recalibration. We found that when the error signal was removed, a change in perceived direction (both visual and proprioceptive) was minimal in all three conditions of optic flow exposure (continuous, intermittent and absent). Although there was a trend for a change in perceived visual direction, this could be accounted for by participants holding an eccentric eye (Paap & Ebenholtz, 1976) or head posture (Grasso et al., 1996).

Given that we found a change in both visual and proprioceptive direction, our results clearly contrast with those of Bruggeman and colleagues (Bruggeman et al., 2007; Bruggeman & Warren, 2010; see Chapter 2 for a summary of their findings). However, our results fit well with Held's hypothesis that an error signal, generated by a discrepancy between anticipated and expected optic flow, is involved in the recalibration of visually perceived direction. The finding of proprioceptive adaptation in the absence of optic flow suggests that some other form of reafferent information might be used to drive a shift in perceived direction. We suggested a few possibilities: namely, positional information (e.g. Andersen et al., 2003) and target drift (Rock, 1966).

Since large magnitudes of adaptation have been found in experiments that have included quite dramatic restrictions on participants' FOV (e.g. Redding and Wallace, 1985a), we suggested that restricting exposure to optic flow may simply slow the recalibration process rather than prevent it. This issue was picked up in Chapter 5.

In Chapter 4, we investigated the effect of cognitive load on the magnitude and site of adaptation. This experiment was based on results suggesting that processing optic flow is attentionally demanding (e.g. Wann, et al., 2000), and research suggesting that cognitive load can impact on the magnitude of recalibration (e.g. Redding & Wallace, 1985a). In reviewing this literature, we highlighted several inconsistencies, and so decided to revisit the issue.

Using the paradigm of Redding and Wallace (1985a) as a starting point, we investigated the impact of cognitive load, while also assessing the relative magnitude of visual and proprioceptive recalibration. Because we expected attentional load to reduce the magnitude of recalibration, we increased the duration of exposure to the displacement from approximately 3 minutes (as used in experiments 1 and 2) to approximately 10 minutes. We found that, similar to Redding and Wallace (1985a), as we increased cognitive load, the magnitude of recalibration (both visual and proprioceptive) decreased. It was concluded that this provided evidence to suggest that processing reafferent visual information is attentionally demanding.

With regards to the magnitude of visual and proprioceptive recalibration we found that, after 10 minutes of exposure, in line with research by Redding and Wallace (1985a), proprioceptive recalibration was much greater than visual recalibration across all levels of secondary task difficulty. This was opposite to the pattern of results reported in Chapter 3 that found more visual than proprioceptive recalibration in a comparable condition. We hypothesised this could be accounted for by visual and proprioceptive recalibration having different timecourses.

To investigate this possibility, using a similar total exposure time to that used in the Attention experiment, in Chapter 5 we measured recalibration at four intervals during prism exposure. To investigate whether exposure to optic flow significantly affected the timecourse of recalibration, the three conditions used in experiment 1 were included (i.e. continuous, intermittent or no flow). In the conditions containing Flow (Flow and StopGo), after the first exposure phase (6 trajectories), change in perceived visual straight ahead reached approximately 2.5°. After extended exposure, visual adaptation did not increase. In the absence of optic flow, visual recalibration gradually increased across exposure phases, eventually reaching a similar magnitude to that obtained when optic flow was available (2.5°). The opposite pattern of results was found for proprioceptive recalibration: a change in proprioceptive straight ahead occurred gradually when optic flow exposure was continuous, yet was present immediately (at the end of the first exposure phase) when optic flow was intermittent, or absent.

The results suggested that, other cues might be used to help recalibrate perceived direction when optic flow is not available. We suggested that the use of an enclosed environment enhanced positional cues, and that these cues could inform the observer that their current locomotor direction was not as expected (e.g. Beusmans, 1998; Andersen et al., 2000). We also suggested the possibility that target drift contributed to the recalibration process (Rock, 1966). Both when optic flow was present and absent, we suggested that participants were using these cues to aid recalibration.

In Chapter 6, we investigated whether the change in perceived direction could be mapped onto a change in target-heading direction. A detailed analysis of the target-heading error (difference between the direction the participant walked, and the position of the target) revealed that adaptation was present in both the initial (1m) heading error across trials, and in the on-going heading error across the course of a trajectory. This result complements other research that has looked at locomotor adaptation (Bruggeman et al., 2007; Bruggeman & Warren, 2010). However, importantly, our findings also contrasted with this previous research in that we revealed that visual recalibration could be mapped onto a change in heading error. The findings presented in Chapter 6 are important in that they offer the first illustration of a *direct* relationship between a change in perceived visual direction and a change in walking direction. They also highlight the primary role of egocentric direction in the visual guidance of locomotion.

In Chapter 2, we noted that both left and rightward displacing prisms were used to induce a misperception of direction in our studies of recalibration. The data presented in chapters 3-6 show the results of both left and rightward displacements combined. In Chapter 7, we outlined the findings of several recent papers suggesting the possibility that adaptation to displacing prisms is asymmetrical, with leftward displacing prisms producing more adaptation than rightward displacing prisms (e.g. Colent et al., 2000; Michel et al., 2008). The aim of Chapter 7 was to fully investigate whether an asymmetry existed in our adaptation data, as well as the trajectory data presented in Chapter 6. Analysis of experiments 1-3 (NoFlow, FOV and Error Signal) revealed that displacement direction (or walking direction, experiment 3) was not a significant source of variance. However, in the two displacement experiments (NoFlow and FOV), there was a trend to suggest more recalibration after leftward displacement exposure.

Two main findings emerged from the asymmetry analysis of the Attention experiment: (i) the effect of cognitive load was more prominent during rightward displacement exposure, and (ii) the magnitude of proprioceptive recalibration was greater after leftward displacement exposure. Similarly, reanalysis of the Timecourse data revealed more adaptation after leftward displacement exposure.

When investigating asymmetries in the heading error of the Timecourse experiment, we revealed an interesting trend: leftward displacement exposure was found to produce smaller heading errors, suggesting a larger change in perceived direction (in line with the recalibration results). Interestingly, this effect was only present when examining conditions that contained optic flow (Flow and StopGo). In the absence of optic flow we found a curious switch in heading error asymmetry: heading error was largest after leftward displacement exposure. A similar pattern of results was found when we investigated the relationship between change in perceived straight ahead and heading error as a function of displacement direction: similar to the data analysis presented in Chapter 6, change in visual straight ahead offered the best representation of change in heading error across exposure phases, but interestingly, only when optic flow was present (Flow and StopGo).

The findings of Chapter 7 offered new insight into the recalibration of perceived visual and proprioceptive recalibration, suggesting that conclusions with regards to the process and end-point of perceptual-motor adaptation are much more complicated than previously described. The left/right breakdown of the relationship between perceived direction and heading error further strengthened the case that a change in visual straight ahead underlies a change in walking trajectory only when optic flow is available. This interesting finding warrants further investigation.

In the final empirical chapter (Chapter 8), we further investigated the role of perceived straight ahead in heading direction; however, rather than using prisms to induce a misperception of direction, we studied two patients whose misperception of direction had clinical roots due to a right hemisphere stroke, and three control patients with similar right hemisphere damage. We found that control patients' perception of visual and proprioceptive straight ahead were accurate prior to exposure to the prisms. Similar to healthy subjects, the control patients' walking trajectories were straight when they were not wearing prisms, and deviated to the left or the right depending on the displacement direction to which they were exposed.

The results of the case study patients are much more difficult to interpret. Although we were able to correct for a curvature in walking trajectory using prisms, both the direction of the curvature, and the direction of displacement used to correct the walking trajectory were found to be at odds with the predictions of the egocentric direction model of walking. The fact that prisms could be used to correct a bias in walking trajectory suggested that perceived direction was related to heading direction. However, due to the small sample size and conflicting results, we suggest that the findings should be taken with caution and should be used as pilot results to inform other experiments.

Critical review of the work reported in the thesis

As reviewed above, several novel and interesting findings have emerged from the work presented throughout this thesis. The finding of a role for optic flow in recalibration while walking is an important one that goes back to a suggestion made by Held and Freedman (1963) almost 50 years ago that, until recently, has not received much empirical testing. Although recent research suggests that optic flow is not involved in the recalibration process (e.g. Bruggeman et al., 2007), here we have presented opposing evidence in line with the original conjecture.

The finding that a change in perceived visual direction relates to a change in walking direction is also an important one in that it bolsters the egocentric account of the visual guidance of locomotion. The optic flow vs. egocentric direction debate is a long-standing one. Here we have outlined a separate role for optic flow, not in the visual guidance of walking, but in the recalibration process. This fits with a growing body of research suggesting alternative uses for optic flow (e.g. Warren & Rushton, 2009). Furthermore, although our patient experiment was not as successful as we would have hoped, it did provide evidence to suggest that inducing a visual shift in perceived direction can modify walking direction.

Although the findings of the research presented in this thesis offer a valuable contribution to the literature, it is important to note a few limitations associated with the experimental design. A possible criticism may relate to the use of a flat surface (the side of a building) to take measures of perceived direction. Indeed, there is evidence to suggest that a flat surface oriented in a particular way can induce a bias in visually perceived eye-level level, and visually perceived straight ahead (e.g. Li, Dallal & Matin, 2001; Harris & Gilchrist, 1976). This is particularly relevant for the VS measure: to reduce the possibility that observers could use a remembered mark on the wall to inform their indications of perceived visual direction, they were required to stand on an angle of either 15 or 30° relative to the surface. A pilot study, revealed that the slanted surface did induce a bias in perceived straight ahead, such that straight ahead appeared to be further along the wall depending on the direction the observer was facing (i.e. if an observer turned to the right, so that the wall was now on their left-hand side, visual straight ahead was perceived to be further rightwards; if an observer turned to the left, so that the wall was now on their left-hand side, visual straight ahead was perceived to be further leftwards).

An effective way to overcome this potential limitation would have been to use a curved surface instead of a flat surface – this would remove any cues offered by the orientation of the wall. However, we did not have one available at the time of testing, and we have no reason to believe this had a significant effect on our findings Although the results of the pilot study revealed that the slanted surface did indeed induced a bias in perceived visual direction; observers were precise in their estimates. Since the same procedure was adopted both prior to and after exposure to the prisms, it is unlikely that the slanted surface had an effect on our results.

There are a couple of procedural issues that require clarification: namely, the different number of experimental trials included in each of the five recalibration experiments, and the reasons for choosing a within vs. a between subjects design. The reduced number of trials in the initial three experiments was based on pilot data indicating that significant effects could be obtained using an exposure duration consisting of only six trajectories. Indeed, there is evidence to suggest that long exposure times are not necessary to obtain large amounts of adaptation (see Redding & Wallace, 1997). A longer exposure duration was chosen for the Attention experiment to increase the chance of obtaining an effect of the secondary cognitive load, and to keep in-line with the procedure adopted by Redding and Wallace (1985a). For the latter experiments (Attention and Timecourse) we switched to a between groups design. Although, ideally, all five experiments would have been conducted within subjects, it was not practical to have participants in the longer experiments walk over 100 trials.

Implications of the research

There are several ways in which future research can capitalise on the findings of this thesis. Having established a central role of optic flow in the rapid recalibration of direction, researchers should be able to maximise/minimise the magnitude of adaptation by reducing or increasing exposure to optic flow accordingly. Any restrictions on exposure to an optic flow field while walking should be noted, since this might reduce the magnitude of recalibration obtained. The finding of an effect of attentional load suggests that researchers should take particular care to note the cognitive demands of their exposure task.

The findings with regards to an asymmetry in adaptation illustrate that researchers should be careful when averaging across displacement directions. However, there remains much to be learned as to why a leftward displacement should produce more adaptation. Indeed, we demonstrated that conducting a secondary cognitive task actually had a more pronounced effect on rightward displacement exposure.

In Chapter 8, we described some interesting findings with regards to a relationship between perceived direction and walking direction in patients with right hemisphere damage. This finding raises important possibilities for the clinical use of prism glasses: a clinician could simply monitor the direction of trajectory curvature and prescribe prism (or 'walking') glasses accordingly. Although the conclusions from this experiment, given the number of patients included, are inevitably speculative, the experiment can be regarded as a pilot study that will inform future research.

Future research

Taken together, the results presented in this thesis offer a compelling account with regards to the role of optic flow in the recalibration of perceived direction, and the use of egocentric direction in the visual guidance of walking. Given the recent debate concerning these two topics it is necessary that future research builds on the findings presented here.

An interesting avenue for future research would be to specifically examine the effect of an enclosed environment on recalibration. This finding would be particularly informative for comparing across studies that use different environmental conditions. There are also a few other cues that we have not considered in great detail; for example, in Chapter 3 (experiment 2 – FOV) we mentioned the possibility that the magnitude of recalibration decreased as a function of observers using the goggles as a reference frame to judge head-centric straight ahead, and not as a result of a spatial reduction in exposure to optic flow. Although we were able to discount this possibility, it is still possible that observers could use the frame of the prism glasses themselves, or the position of their nose and eye orbits, which always remained visible during the adaptation period, to make judgement of straight ahead. With regards to the frame of the glasses, this would be an extremely difficult caveat to remove. The only possibility would be to use contact lenses containing prisms, but it is likely that the lenses would be too heavy to remain in the desired position on the eye. With regards to using the position of the nose and eye-orbits, there is evidence to suggest that these have little influence on judgements of straight ahead (e.g. Shebilske & Nice, 1976).

It will also be important for future studies to use more controlled environments to specifically examine several factors that we were unable to control for: for example, did the measure of visual straight ahead involve a change in felt eye position, or felt head position? Would we find the same results if we used a measure that did not involve a reference to 'straight ahead', but instead required observers to point to an unseen body part (e.g. Templeton et al., 1974; Howard, 1982)? What is the specific contribution of motion parallax to recalibration in the walking observer (i.e. can motion parallax account for the lack of adaptation found in experiment 3 – the lights experiment)? Furthermore, given that proprioceptive adaptation was found to be unrelated to the direct effects of the prismatic exposure, it will be a fruitful avenue for future research to determine the significance of this shift.

It is also important to replicate the results presented in Chapter 6 demonstrating that a change in visual direction can be directly mapped on to a change in walking direction, although interestingly, only when optic flow is available. This finding lends considerable support to the egocentric direction account of the visual guidance of locomotion, and is, to our knowledge, the first evidence to suggesting a direct relationship between these two variables. It is thus imperative that this finding is replicated, perhaps including more inter-trial measures of perceived straight ahead, or using longer exposure times, to allow a comparison to be made over more data points. Here we bracketed the data to overcome the disruptive effects of walking to the measurement area after the exposure period, a more efficient method would be to have participants give estimates of perceived straight ahead in the same position in which the trial ends (without having to move away from the experimental area).

Finally, the puzzling patient findings presented in Chapter 8 need to be readdressed. Although the findings were contradictory, we were able to find a change in walking direction as a result of the induced shift in perceived direction in both case study patients, suggesting a possible role for perceived direction in the visual guidance of walking. The conclusions made here were inevitably speculative; however, a study incorporating a larger sample size and both measures of perceived visual and proprioceptive direction would be much more informative.

Overall conclusions

(1) What is the role of optic flow in the recalibration of perceived direction?

The results of this thesis suggest that optic flow is involved in the rapid recalibration of visual straight ahead: when exposure to optic flow was restricted, both spatially and temporally, we found a reduction in the magnitude of visual recalibration. We also presented results to suggest that processing optic flow is attentionally demanding, such that when cognitive capacity was reduced, the magnitude of recalibration was also reduced. When optic flow was not available some recalibration still occurred, suggesting that other cues could be recruited; however, this recalibration was primarily proprioceptive in nature, and took longer to develop

(2) What is the relationship between perceived direction and walking direction?

Our findings offer convincing evidence to suggest that perceived direction and heading direction are closely linked, such that a change in visual direction produces a change in walking direction. We demonstrated this both in our trajectory analysis (Timecourse experiment), as well as in a study of two patients whose perception of straight ahead was biased as a result of a right hemisphere stroke.

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Appendix 1: Details of trajectory extraction

By Dr. Cyril Charron

Acquisition and storage of the raw videos

Videos were acquired using an interlaced camera mounted on a support on the 12th floor of a surrounding building. The videos were later digitized and converted to a compressed format using QuickTime (format was MPEG4 AVC). The video resolution was fixed at 720x576.

Extraction of the trajectories

The trajectories were extracted in a semi-automated way using a Matlab interface. A background subtraction method was first applied to remove the stable parts in the scene, (i.e. ground, buildings, and to segment out the participant). A normalised cross correlation tracker was then applied to track the head of the participant across the video. Pixel positions were stored in a file for later processing and analysis.

Calibration of the camera

In order to retrieve the trajectories of participants in the world reference frame, we estimated the intrinsic (focal length, optical centre and pixel size) and extrinsic parameters (rigid transformation between the camera reference frame and the world reference frame) of the camera. We used the calibration method from Zhang, which allows using calibration points within a single plane, in our case the corners and target landmarks lying on the ground. After retrieving the homography between the world points and the image points, intrinsic and extrinsic parameters of the camera are retrieved.

We used the Camera Calibration Toolbox, and tuned the optimization parameters so that Zhang's method worked with a single image (while a dozen is usually required, and a least three are needed to estimate all the camera parameters). To do so, we forced the pixels to be square and the optical centre to coincide with the image centre in the model. This calibration procedure was applied for every session.

Retrieving the 3D position

Thanks to the camera calibration, the position of the participant could be retrieved in the world coordinates. The size of the participant was fixed to 1.70m to constrain the projection from the camera frame to the world frame.

Aligning the data

The obtained data were then parsed in terms of trials. Then a reference frame was defined for each trial. The abscises were defined as the axis passing by the starting point of the participant and the target of trial. The ordinate axis was then define as the orthogonal axis to the abscises (direct orientation). Each trial was projected onto its corresponding reference frame to obtain aligned data.

Filtering

The data were smoothed using a 2D Kalman filter with constant speed.

Heading error

The heading error is defined as follows:
Where theta_S is the direction the participant is moving to (straight ahead i.e. the tangent to the trajectory, obtained by differentiating the aligned trajectories), and theta_T is the angle between the abscises axis and the line joining the participant position and the target.

Resampling

Finally the data were re-sampled spatially to allow us analyzing the trajectories together. A bilinear interpolation was applied to the aligned data and to the heading trajectories.