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The Coupling of Vision with Locomotion in Cortical Blindness

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Short title: Visuo-Locomotor Coupling in Cortical Blindness

Abstract

Maintaining or modifying the speed and direction of locomotion requires the coupling of the locomotion with the retinal optic flow that it generates. It is shown that this essential behavioral capability, which requires on-line neural control, is preserved in the cortically blind hemifield of a hemianope. In experiments, optic flow stimuli were presented to either the normal or blind hemifield while the patient was walking on a treadmill. Little difference was found between the hemifields with respect to the coupling (i.e. co-dependency) of optic flow detection with locomotion. Even in the cortically blind hemifield, faster walking resulted in the perceptual slowing of detected optic flow, and self-selected locomotion speeds demonstrated behavioral discrimination between different optic flow speeds. The results indicate that the processing of optic flow, and thereby on-line visuo-locomotor coupling, can take place along neural pathways that function without processing in Area V1, and thus in the absence of conscious intervention. These and earlier findings suggest that optic flow and object motion are processed in parallel along with correlated non-visual locomotion signals. Extrastriate interactions may be responsible for discounting the optical effects of locomotion on the perceived direction of object motion, and maintaining visually guided self-motion.

1.0 Introduction

The relationship between perception and action has been of long-standing interest to researchers concerned with both visual processing and motor control. Indicative of their co-dependence is evidence that locomotion can induce changes in the perceived speed of concurrent optic flow (Pelah & Barlow, 1996; Thurrell, Pelah & Distler, 1998; Thurrell & Pelah, 2002, 2005; Durgin, Gigone & Scott, 2005), that changes in optic flow speed while walking at a constant speed can signal an impending collision (Lee, 1980), and that locomotion can change involuntarily in response to changes in optic flow (Prokop, Schubert & Berger, 1997; Dong, Pelah, Cameron & Lasenby, 2008).

Perhaps the most important aspect of the on-line coupling of optic flow detection and locomotion is that they interact recursively. That is, locomotion generates an optic flow pattern on the retina, changes in the optic flow pattern produce changes in the speed and/or direction of locomotion, which in turn changes the optic flow pattern, and so on. The function of this dynamic co-dependence is to maintain (or modify) walking speed and/or walking direction (heading) in response to stability (or change) in the locomotion-generated optic flow pattern (Held & Freedman, 1963; Gibson, 1950; Warren & Hannon, 1988).

A noteworthy feature of locomotion in normally sighted individuals is that retrospectively (and introspectively) episodes of walking seem to have taken place without conscious awareness or attention to the optic flow pattern that had been generated by the locomotion. This effect, together with observations that a surprising degree of visual control of locomotion can be retained in cortical blindness (Humphrey, 1974; de Gelder et al. 2008), suggests that the optic flow induced by locomotion may

be processed without access to the pathways mediating conscious visual awareness. The objective of this study is therefore to determine whether behavior requiring the detection of optic flow and its inherent coupling with locomotion are preserved, despite the absence of processing in Area V1 and the accompanying loss of conscious awareness.

This objective was addressed by testing a hemianope, an individual for whom unilateral damage to the striate cortex (Area V1) has resulted in the loss of object/shape perception and conscious awareness for stimuli presented in the contralateral hemifield (Barbur, Ruddock & Waterfield, 1980; Weiskrantz, 1986; Barbur et al. 1993), the ipsilateral hemifield having remained normally sighted and thus acting as a control. During trials, optic flow stimuli were presented to either the normally sighted or the cortically blind hemifield whilst the hemianope was walking on a treadmill. Evidence for partial sparing of direction discrimination for a variety of moving stimuli (e.g., Barbur et al. 1993; Azzopardi & Cowey, 2001) led to the expectation that optic flow motion could also be processed in the cortically blind hemifield. What is unique about the current study is that rather than direction discrimination, as in earlier studies, it is aimed at showing that this kind of unconsciously detected motion is coupled with an essential behavior, locomotion.

The further possibility that there are independent pathways for the processing of optic flow and object motion was suggested by evidence for qualitative differences in the stimulus information that serves as a basis for direction discrimination in the cortically blind and normally sighted hemifields. That is, Azzopardi and Hock (2011) found that direction discrimination within a hemianope's blind hemifield was based on

the detection of spatio-temporal changes in "raw" luminance (Chubb & Sperling, 1989),

or more generally, 1st-order motion energy (Adelson & Bergen, 1985), whereas

direction discrimination within his normally sighted hemifield relied on the detection of

changes in shape (although motion energy extraction remained possible as well).

Treadmill walking was essential for this study because it disrupts the normal

correlation between locomotion speed and optic flow speed (Pelah & Barlow, 1996); on

a treadmill, faster walking no longer automatically results in faster optic flow. Under

these open loop conditions, optic flow on the retina is not affected by walking speed,

and thus, the lack of conscious awareness of an optic flow pattern cannot be attributed

to compensatory mechanisms that discount or cancel the retinal motion signal via

matching walking-speed determined efferent or afferent motor information (Andersson

et al. 1981; Thurrell & Pelah, 2005; Tcheang, Gilson & Glennerster, 2005), nor to an

internal template of the optic flow pattern for different locomotion speeds (Perrone,

1992).

Obtaining evidence for visuo-locomotor coupling when optic flow stimuli are

presented within the hemianope's cortically blind hemifield, where there is no feed

forward projection to Area V1, and no conscious awareness of the stimuli, would then

indicate that retinal optic flow signals have reached extrastriate areas via neural

pathways that by-pass Area V1. In the macaque, these pathways involve the superior

colliculus of the midbrain (Gross, 1991; Mohler & Wurtz, 1977) and/or direct

connections from the lateral geniculate nucleus (Cowey & Stoerig,1989; Schmid et al.

2010) to extrastriate areas.

The extrastriate targets for pathways through Area V1 and pathways that by-pass Area V1, include directionally selective motion detectors in macaque Area MT (Newsome, Mikami & Wurtz, 1986). Cooling or lesioning Area V1 leaves a high proportion of MT neurons active, and the additional destruction of the superior colliculus completely eliminates MT activation (Rodman, Gross & Albright, 1989, 1990). Significantly, directionally selective Area MT motion detectors project onto optic flow detectors in Area MSTd (Tanaka & Saito, 1989; Yu et al. 2010).

Three experiments are described in which the cortically blind and normally sighted hemifields of the hemianope were compared in order to determine behaviorally whether visuo-locomotor coupling could be based on the processing of optic flow along neural pathways that by-pass Area V1, independently of conscious awareness of the optic flow stimulus, and independently of motion processing along the geniculostriate pathway.

2.0 Methods

2.1 General method

Testing was done with an individual, denoted as GY, who suffered damage to his occipital lobe following an automobile accident at the age of 8 years that resulted in unilateral loss of function in his left primary visual cortex (Area V1). He is functionally hemianopic, with less than 3 deg macular sparing, probably due to spared tissue in the occipital pole (Barbur, Ruddock & Waterfield, 1980). As illustrated in Figure 1a, testing was done with a locomotion simulator composed of a Woodway Exo43 treadmill facing a large translucent screen (Pelah et al. 1998). Optic flow stimuli were rear-projected onto the screen by an InFocus LP740 LCD projector with a resolution of 1024 by 768

pixels and a refresh rate of 70 Hz, updated on alternate frames (the projection covered a visual area of 93 x 77 deg). Movement on the treadmill was not motorized. Its belt was composed of low-friction rolling slats, so GY's self-generated locomotion required minimal exertion. Whether walking or standing, the viewing distance to the center of the screen was approximately 90 cm.

The optic flow stimulus was composed of a set of 15 nested, concentric square frames that radiated outward to create the appearance of walking through a corridor. Consistent with the laws of perspective, the frames varied in diameter and thickness as the inverse tangent of their simulated distance from the observer. The innermost frame intercepted a visual angle of 19.0 deg and was 1.2 deg thick. The outer-most frame intercepted a visual angle of 77.0 deg and was 2.4 deg thick. The radially expanding motion was faster for the outer than the inner squares (as measured in the plane of the display). The optic flow speeds indicated for each experiment were characterized by the speed measured at the mid-hemifield position of the stimulus, approximately 27.8 deg from fixation (indicated by the broken line in Figure 1b).

The luminance values of the nested squares varied with eccentricity. It was dimmest (0.1 cd/m^2) for the innermost frame, simulating it being the furthest square from the perceiver when expanding optic flow results from forward walking. As the frames radiated outward, their luminance gradually increased to 1.9 cd/m^2 at their mid-hemifield location, and gradually decreased to the background luminance of 0.01 cd/m^2 as the square frames continued radiating outward toward the display's periphery. When the outer-most frame disappeared, it was immediately replaced by the presentation of the smallest square frame in the center of the display. The gradual
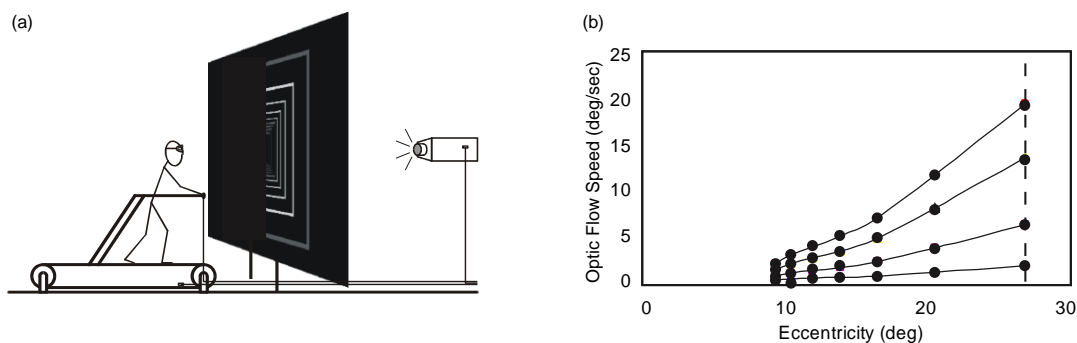
Figure 1
(Caption is on the last page of manuscript)

changes in luminance minimized luminance transients, and in particular, edge flicker in

the far periphery. In different experimental conditions, luminance values were reduced

from the above values by placing neutral density filters in front of the lens of the LCD

projector. Goggles were worn in order to shield GY's left eye and occlude peripheral

distractions.

The left and right halves of the nested squares stimulus were presented during

separate blocks of trials, directed respectively at either the normally sighted or the

cortically blind visual hemifield. The experiments were conducted following 30 min of

dark adaptation. GY was instructed to maintain fixation on a small square (0.28 x 0.28

deg; luminance = 1.5 cd/m^2) at eye level in the center of the display. Self-propelled

walking speeds were measured with a sensor attached to the treadmill. The time series

of walking speeds was low-pass filtered and the average speed determined over the

last 5 sec of each walking interval. No part of the stimulus was presented within a 3.5

deg radius circular arc surrounding the fixation square in order to ensure that the

stimulus was outside GY's spared macula region of the retina, which responds to visual

information in both the blind and sighted hemifields (Barbur et al. 1980).

2.2 Monitoring eye fixation

GY previously participated in numerous psychophysical studies that required

fixation at a specified location, most of which confirmed fixation by visual inspection.

Quantitative measurements by Weiskrantz, Harlow and Barbur (1991) indicated that he

could maintain fixation to within approximately +/- 0.5 deg. Whether fixation could also

be maintained while GY was walking on a treadmill was determined in this study with a

head-mounted Epic 1-Diamond IR Limbus Eye Tracker, which detected horizontal eye

movements with respect to the fixation point. These measurements were made while

GY's head was placed in a chin rest while walking on the treadmill. Despite the head

movements produced by the locomotion, GY maintained fixation to within +/- 2.0 deg,

well enough that random fluctuations in eye position were too small to displace portions

of the optic flow onto his spared macular region. Fixation was monitored by the visual

inspection of GY's eyes throughout all three experiments.

2.3 Conscious awareness

After each trial, GY indicated whether or not he was aware of the optic flow

stimulus. He reported full awareness when it was presented in his normally sighted

hemifield, but not in his cortically blind hemifield. His reports for blind hemifield

presentations may have reflected both Type 1 blindsight, for which there is no

conscious awareness whatsoever, and Type 2 blindsight, for which there is no

conscious awareness of the stimulus, but there is an awareness that "something is

happening" (Weiskrantz, Barbur & Sahraie, 1995). Barbur et al. (1994) have shown

that GY can exhibit both types of blindsight, depending on the stimulus discrimination required. In Experiment 1 of the current study, no discrimination was required of GY when he was walking on the treadmill while optic flow was presented in either his normally sighted or cortically blind hemifield. Type 1 blindsight, with no conscious awareness whatsoever, is therefore possible for his blind hemifield. In Experiments 2 and 3, GY was required to discriminate between different optic flow speeds by walking at a speed that matched the optic flow speed; Type 2 blindsight was therefore possible here. However, at the start of each trial in each of the last two experiments GY had to be told when to start walking, even though the optic flow stimulus was already presented in his cortically blind hemifield. He also had to be told when to stop walking at the end of a trial after the stimulus was gone. He was unable to distinguish the optic flow stimulus from a blank screen, was indicative of Type 1 blindsight. Because GY's reports of no awareness of the optic flow stimulus could have reflected either type of blindsight, we have taken the conservative position that the results reflect Type 2 blindsight.

3.0 Experiment 1: Locomotion and Judgments of Optic Flow Speed

Most experimental and computational analyses of optic flow processing have been concerned with the distortion of locomotion-generated optic flow patterns by eye movements, and its resulting effect on the perception of heading (e.g., Warren & Hannon, 1988; Warren et al. 2001). Much less frequent are studies examining the relationship between optic flow and the motor-related signals of locomotion. Many of the latter have been concerned with the involuntary effects of optic flow variations on

walking speed and gait patterns (Pailhous, et al. 1990; Konzak, 1994; Prokop et al.

1997; Dong, et al. 2008). Experiment 1 of the current study was concerned with the

reverse, i.e., the effect of locomotion speed on the perception of optic flow. That is,

while open-loop treadmill walking speed does not affect the retinal speed of an

independently presented optic flow stimulus, it does affect its *perceived* speed. The

'speeding-up' of perceived optic flow occurs while walking in a normal environment

following a period of treadmill walking in the absence of optic flow (Pelah & Barlow,

1996), and the 'slowing down' of perceived optic flow occurs *during* treadmill walking in

the presence of optic flow (Thurrell et al. 1998). For the latter, the more rapid the

treadmill walking, the slower the physically constant optic flow appears (Thurrell let al.

1998; Thurrell & Pelah, 2002, 2005; Durgin et al. 2005).

It was determined in this experiment whether the slowing effect of walking speed on

perceived optic flow speed, an indicator of visuo-locomotor coupling, would be

observed in GY's cortically blind as well as his normally sighted hemifield. This was

determined by presenting optic flow stimuli to either hemifield while he was walking on

a self-propelled treadmill at one of six self-selected speeds.

3.1 Method

Each trial began with a written instruction on the screen indicating the subjective

walking speed required of GY for that trial: either 'stationary', 'very slow', 'slow',

'normal', 'fast', or 'very fast'. Five sec was provided for GY to reach his self-selected

walking speed according to the instruction. This was followed by a 10 sec interval

during which a vertically split expanding optic flow stimulus with a speed of 2.7 deg/sec

(measured for the frame at the mid-hemifield position) was presented to either his

cortically blind or normally sighted hemifield. Immediately after the 15 sec interval,

while now standing stationary on the treadmill, GY adjusted the speed of an optic flow

stimulus presented in his normally sighted hemifield so that it reproduced the

remembered speed of the optic flow stimulus during the preceding walking episode.

The initial setting for each 10 sec test was at a randomly selected optic flow speed.

The average speed-matching setting was determined over the final 1 sec of the 10 sec

speed-setting interval. There were a total of 18 randomly ordered trials, 3 for each of

the 6 subjective walking speeds, presented first in GY's normally sighted hemifield, and

then for two blocks of 18 trials in his cortically blind hemifield. Before testing, GY

practiced walking on the treadmill in response to the six different speed instructions.

3.2 Results

The effect of locomotion speed on the perceived speed of accompanying

optic flow was measured by the post-locomotion reproduction of that optic flow speed.

Remarkably, faster walking resulted in the perceived slowing of optic flow, even when

the optic flow was presented in GY's cortically blind hemifield, Moreover, the slowing

effect in the blind hemifield was similar to that obtained in the normally sighted

hemifield; for both the fastest walking resulted in the constant-speed optic flow stimulus

appearing to be stationary. The negative correlation between walking speed and

perceived optic flow speed was significant for the normally sighted hemifield, $r(16) = -0.92$, $p < 0.001$ (Figure 2a), as well as for the first block, $r(16) = -0.78$, $p < 0.001$, and

second block, $r(16) = -0.91$, $p < 0.001$, of trials for the cortically blind hemifield (Figures

2b and 2c). However, the hemifields differed in their sensitivity to the differences in

optic flow speed. This was indicated by the slopes of the regression lines being flatter

EXPERIMENT 1
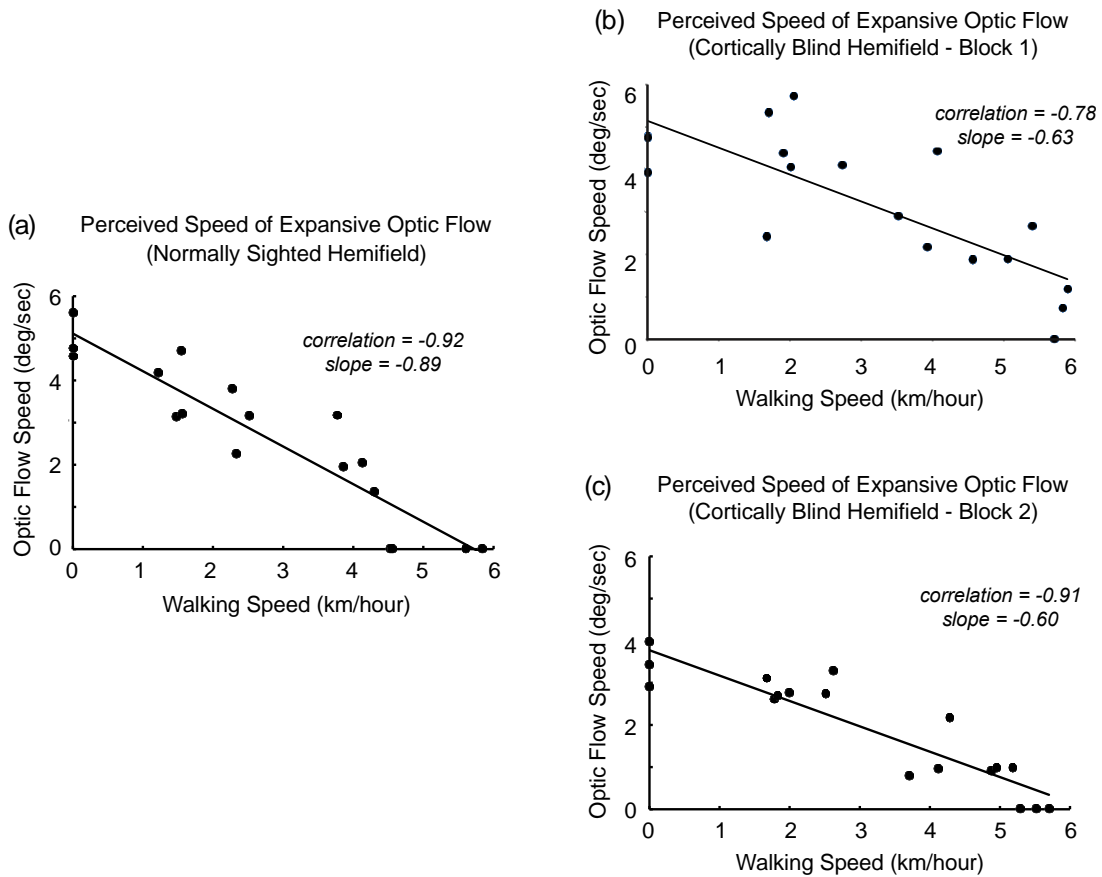
Figure 2
(Caption on last page of the manuscript)

for the two blocks of blind-hemifield trials (slope = -0.63 and -0.60) than for the

normally sighted hemifield trials (slope = -0.89). The reduced sensitivity to differences

in speed in the blind hemifield was not surprising given the substantial loss in

spatiotemporal contrast sensitivity in GY's cortically blind hemifield (Cowey, 2010).

3.3 Additional results – verbal ratings of optic flow speed

The results of Experiment 1 are indicative of optic flow being detected, under the influence of walking speed, in GY's blind hemifield. Alternatively, it might be argued that GY detected nothing useful in his cortically blind hemifield, and that instead his post-locomotion judgments of optic flow speed in his blind hemifield were derived from visual memories from earlier judgments of optic flow speed in his sighted hemifield. That is, the apparent slowing effect of locomotion speed on the perceived speed of the optic flow presented in GY's cortically blind hemifield may have been due to visual memories associated with similar locomotion speeds during earlier testing in his normally sighted hemifield.

Contrary to this possibility, there is clear evidence that differences in stimulus speed can be discriminated in cortically blind hemifields (Barbur, Ruddock & Waterfield, 1980; Morland et al. 1999*).* The purpose of this additional experiment was to confirm these earlier findings with the optic flow stimuli tested in the current study.

GY judged four randomly ordered speeds of expanding optic flow (4.0, 7.0, 10.0 and 13.0 deg/sec) while standing stationary on the treadmill. After each 10 sec presentation, he verbally rated the speed of the optic flow on a scale from 1 to 4, with 4 denoting the fastest and 1 the slowest speed. There were 160 trials (40 for each of the 4 optic flow speeds) separately for his sighted and blind hemifields. The luminance of the square frame near the mid-hemifield location was 0.005 deg/m^2. Consistent with previous studies, these judgments were made while GY was stationary. Behavioral discrimination of optic flow speeds in his cortically blind hemifield, as indicated by walking, was tested in Experiments 2 and 3.
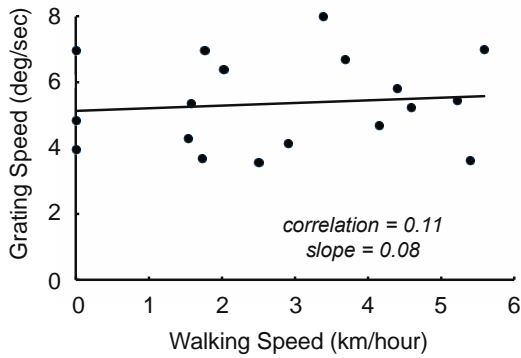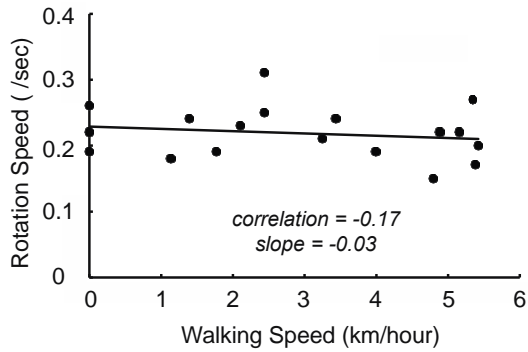
EXPERIMENT 1 (Additional Results)

(a)   (Ratings of Speed for Optic Flow Stimuli)
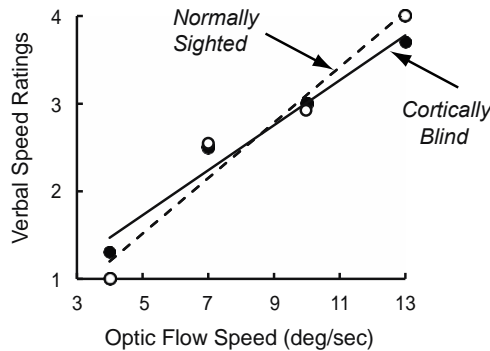
(b) Perceived Speed of Drifting Grating
(Cortically Blind Hemifield)

correlation = 0.11
slope = 0.08

(c) Perceived Speed of Rotating Cartwheel
(Cortically Blind Hemifield)

correlation = -0.17
slope = -0.03

Figure 3
(Caption is on last page of the manuscript)

It can be seen in Figure 3a that GY was able to verbally discriminate optic flow speeds approximately equally well in his cortically blind and normally sighted hemifields. With detected optic flow speeds differentially encoded in his blind hemifield only moments before the sighted-hemifield reproduction test for a trial, it is very unlikely that GY instead based his judgments of optic flow speed in his blind hemifleld on perceived speeds recalled from a preceding block of sighted-hemifield trials, which occurred six or twelve minutes prior to the two blocks of blind-hemifield trials. It can be

concluded, therefore, that locomotion does indeed slow the perceived speed of

detected optic flow more than slower locomotion (as indicated by the negative slopes in

Figure 2), regardless of whether the optic flow is presented in the normally sighted or

cortically blind hemifield.

3.4 Additional results – locomotion with non-optic flow stimuli

A further experiment determined whether the slowing effect of locomotion on the

perception of speed is specific to optic flow stimuli, as would be expected if this

evidence for visuo-locomotor coupling were relevant to visually guided locomotion in

the natural environment. To determine whether this was the case, testing for

locomotion induced slowing was done by presenting, in the cortically blind hemifield, a

downward drifting, horizontally-oriented rectangular grating, and a rotating cartwheel

stimulus, neither of which can be generated as optic flow by forward locomotion.

As in the main experiment, nothing but the fixation mark was presented within a

3.5 deg diameter arc surrounding the macula. The grating had a fundamental spatial

frequency of approximately 0.4 cycles/deg and a speed of approximately 2.5 deg/sec.

It was composed of 15 equally spaced, anti-aliased bars (luminance = 1.5 cd/m^2)

presented against a dark (0.006 cd/m^2) background. In order to minimize luminance

transients and edge flicker, as each bar appeared at the top of the display and then

drifted downward, its luminance gradually increased to a constant level, and then

gradually decreased until the bar disappeared at the bottom of the screen. The

cartwheel was composed of 15 spokes (luminance = 1.5 cd/m^2), rotating

counterclockwise at a speed of 2.7 deg/sec. There were 18 randomly ordered trials for

both the grating and the cartwheel (3 repetitions of the 6 subjective walking speeds).
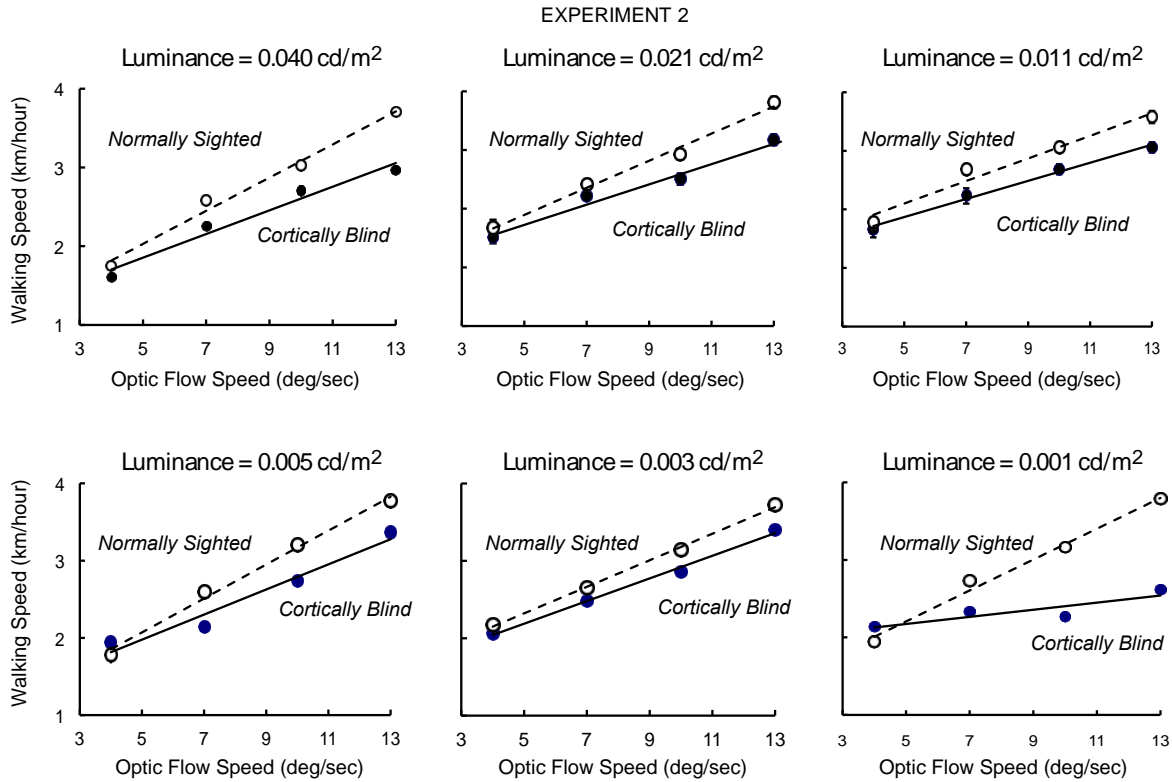
EXPERIMENT 2

Figure 4
(Caption on last page of the manuscript)

As in Experiment 1, after each locomotion episode, GY, standing stationary on the

treadmill, adjusted the grating (or cartwheel) speed presented in his sighted hemifield

so that it matched the remembered speed of the drifting grating (or rotating cartwheel)

during the immediately preceding locomotion episode. It was found that there was no

effect of locomotion speed on the perceived speed of either the drifting grating or the

rotating cartwheel (Figures 3b and 3c). Thurrell and Pelah (2002) have reported similar

results with unimpaired subjects.

These additional results indicate that the slowing effect is specific to the

engagement of locomotion with optic flow stimuli. It is not a general bias due to

concurrent locomotion that affects the perception of speed for any moving stimulus, and in particular, it is not a processing bias peculiar to the cortically blind hemifield.

Because the slowing effect was obtained for optic flow stimuli presented in GY's cortically blind hemifield, it could be concluded that visuo-locomotor coupling can occur without the geniculostriate pathway, and thus, without the associated conscious awareness of the optic flow stimulus. Because it was obtained under the open loop conditions of treadmill walking, it indicated that (unconscious) visuo-locomotor coupling can occur irrespective of matched compensatory mechanisms that discount or cancel optic flow.

4.0 Experiment 2: Matching Walking to Constant Optic Flow Speed

Experiment 1 showed that locomotion induced perceptual slowing can occur in both GY's normally sighted and cortically blind hemifields. On the basis of this evidence for similar visuo-locomotor coupling in the two hemiflelds, it was next determined whether GY would be able to match his treadmill walking speed to the optic flow speed despite the absence of the genicuolostriate projections and Area V1 processing for his cortically blind hemifield.

The luminance of the nested square frames composing the expanding optic flow stimulus was made progressively dimmer during successive blocks of trials in order to minimize the possibility that locomotion matches for stimuli presented in GY's blind hemifield would benefit from light scatter into his sighted hemifield (King et al. 1996).

4.1 Method

Neutral density filters were used to create luminance levels of 0.040, 0.021,

0.011, 0.005, 0.003, and 0.001 cd/m^2, as measured for the brightest square frame near the mid-hemifield location of the expanding nested squares. Although the squares were dim, they were within the range of visibility following a 30 min dark adaptation period as confirmed by sighted hemifield controls. Blocks of 24 order-randomized trials were determined by presenting each of the four optic flow speeds (4.0, 7.0, 10.0 and 13.0 deg/sec) six times. Six blocks of these 24 trials, one for each of the 6 luminance levels were repeated 5 times in the normally sighted hemifield, then 10 times in the cortically blind hemifield. During each trial GY was instructed to match his walking speed to the optic flow speed.

4.2 Results

GY's ability to match the speed of his walking to the speed of the optic flow stimulus was similar in the two hemifields (Figure 4). For each hemifield and each luminance level, GY's average walking speeds were highly correlated with the physical speed of the optic flow. With one exception (the lowest luminance level stimulus in the blind hemifield) the correlations were greater than 0.95 [Footnote 1]. The regression lines for each of the six luminance levels were somewhat flatter for the cortically blind than the normally sighted hemifield. Thus, as in Experiment 1, optic flow speeds were better differentiated in the normally sighted hemifield.

5.0 Experiment 3: Matching Walking to Changing Optic Flow Speed

As discussed in Section 1.0, to be functional in the natural environment it is crucial for locomotor mechanisms to respond on-line to *changes* in optic flow speed. It
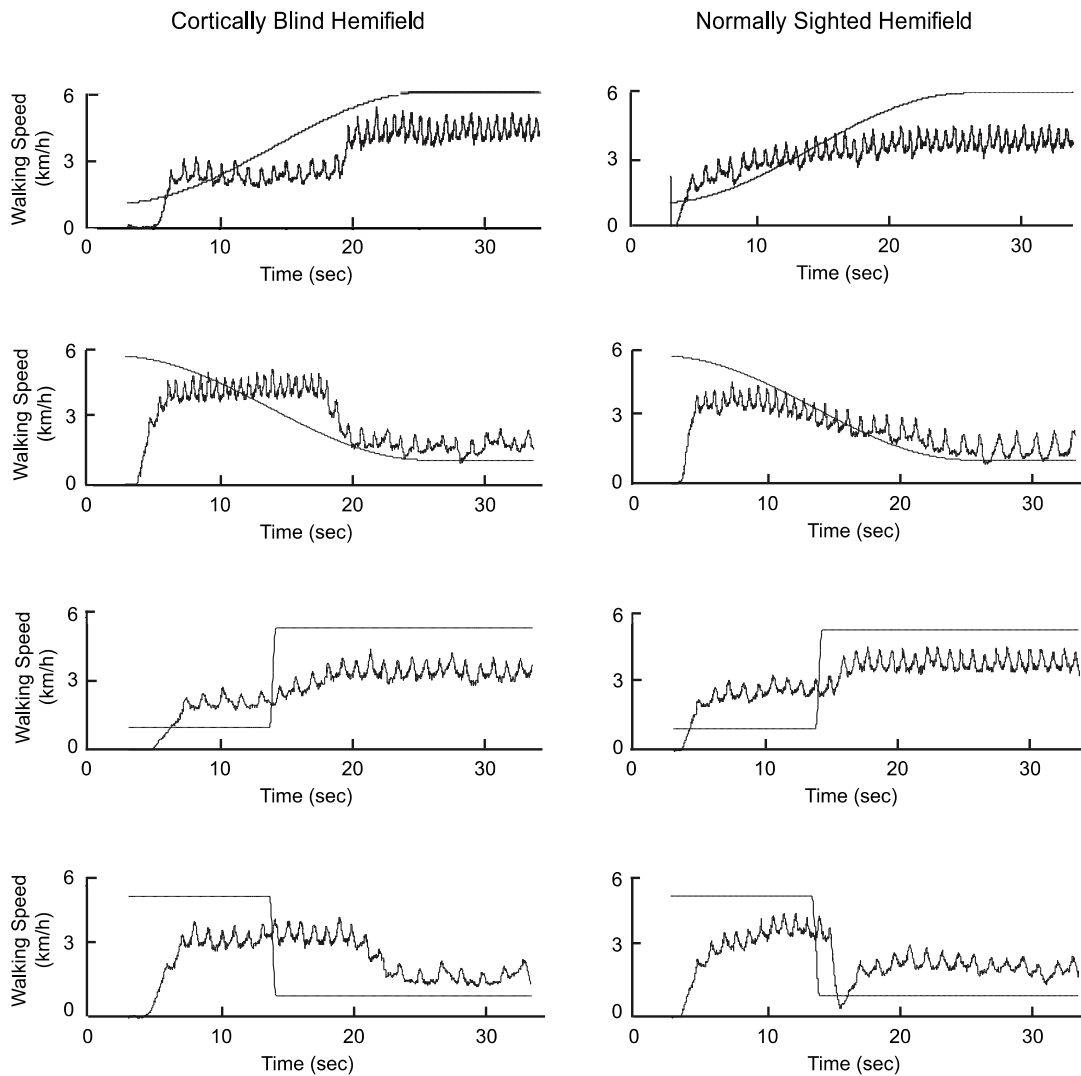
EXPERIMENT 3

Figure 5.
(Caption on the last page of the manuscript)

was determined in this experiment whether this can also occur without the

geniculostriate projections to Area V1.

5.1 Method

Four distinctive stimuli, each repeated five times, were used to test whether GY

was able to match his walking speed to changing optic flow speed in his cortically blind

as well as his normally sighted hemifield. The changes in speed were either abrupt or

gradual, and either increasing or decreasing. Abrupt changes entailed a steep linear

increase (decrease) from 2 to 19 deg/sec (19 to 2 deg/sec) during a 0.3 sec interval in

the middle of a 24 sec trial. Gradual changes in optic flow speed were sinusoidal,

between 2 and 19 deg/sec over the full 24 sec. As in Experiment 2, GY was instructed

to match his walking speed to the speed of the optic flow stimulus in both his normally

sighted and cortically blind hemifields.

5.2 Results

GY was able to modify his walking speed in approximate correspondence to

both gradual and abrupt changes in optic flow speed, regardless of whether the speed

increased or decreased. In his blind hemifield, the average difference in walking speed

between the fast and slow phases of the changing optic flow stimulus was statistically

significant; t(3) = 12.3, p< .001.[Footnote 3]. That is, it was reliably obtained despite

differences in the type of optic flow change (gradual-increase, gradual-decrease,

abrupt-increase or abrupt-decrease). This also was the case when these stimuli were

tested in his sighted hemifield; t(3) = 13.1, p< .001.

It can be seen for the individual trials presented in Figure 5 that his normally

sighted and cortically blind hemifields were similar with respect to the magnitude of

change in GY's walking speed, but the changes in walking speed were relatively

delayed in his blind hemifield. Further research will be required to determine whether

delayed responses to changes in velocity (i.e., changes in speed and/or direction) is a

general characteristic of hemianopic vision that results from the absence of V1

processing.

6.0 General Discussion

Visuo-locomotor coupling occurs whenever we walk in a natural environment. Locomotion creates optic flow on the retina, which in turn is used to maintain or change locomotion in a selected direction and at a selected speed. Visuo-locomotor coupling also occurs while walking on a treadmill, where it takes the form of locomotion-induced slowing of perceived optic flow speed (Experiment 1), and on matching walking speed to constant or changing optic flow speed (Experiments 2 and 3). The results of the current study show that during visuo-locomotor coupling neither the slowing effect nor speed matching requires processing in the geniculostriate pathways that sustain conscious awareness of visual stimuli. These results are unique in comparison with other studies of hemianopic vision, which typically involve simple discriminations (e.g., upward vs. downward motion). Evidence was obtained here for the sparing of optic flow detection coupled with an essential behavior, locomotion. It is noteworthy that this linkage with locomotion seems to be specific to the detection of optic flow. Evidence for locomotion-induced perceptual slowing was not observed for stimuli (vertically drifting gratings and rotating propellers) presented in the cortically blind hemifield (Section 3.3; see Thurrell & Pelah, 2002; 2005; for normally sighted subjects). These stimuli are not generated by locomotion.

Because of unilateral damage to Area V1 of the hemianope, these results indicate that visuo-locomotor coupling can be based on the processing of optic flow in neural pathways from retina to Area MT that by-pass Area V1 (likely through the superior colliculus and/or the lateral geniculate nucleus), probably following on to optic

flow sensitive neurons in homologous Area MSTd (Tanaka & Saito, 1989; Yu et al.

2010) and the posterior parietal cortex for visuo-motor coordination (Milner & Goodale,

1993; Andersen, Snyder, Bradley & Xing, 1997). Given that processing in Area V1 is

deemed necessary for conscious visual awareness (Lamme, 2001; Silvanto et al.

2005), the evidence obtained without Area V1 indicates that conscious awareness of

the optic flow stimulus is not necessary for its coupling with locomotion. It can be

inferred that introspective reports of lack of awareness or attention to optic flow during

locomotion in natural environments may be due to the predominance of activity in

neural pathways that by-pass Area V1.

6.1 Limitations in hemianopic vision

While the hemianope (GY) tested in these experiments reported no conscious

awareness of the stimulus in his cortically blind hemifield, it remains uncertain whether

these reports reflected a complete absence of conscious awareness (see Section 2.3).

This notwithstanding, it has been well-established for GY and other hemianopes that

their perceptual capabilities are typically very different for stimuli presented in their two

hemifields, in that there are substantial blind-hemifield deficits for the discrimination of

numerous visual attributes (Barbur, Harlow & Weiskrantz, 1994; Cowey, 2010).

Notably, the usual hemifield asymmetry was much reduced in the current study, which

found that visuo-locomotor coupling is similar in the cortically blind and normally

sighted hemifields. The observed similarity of the hemifields suggests that neural

pathways in which locomotion-induced optic flow is processed can function

independently of the (in this case, damaged) geniculostriate pathway to Area V1. The

relatively small deficits in the differentiation of optic flow speeds in the cortically blind

hemifield may have been due to the hemianopic loss in spatiotemporal contrast sensitivity in the absence of Area V1 processing (Barbur et al. 1994; Cowey, 2010), or to the absence of feedback from damaged Area V1 to subcortical nuclei that affect contrast sensitivity (Przybyszewski et al. 2000; Cudeiro & Sillito, 2006).

Alternatively, it is possible that GY's speed-matching deficits in his cortically blind hemifield were due to the absence of Area V1 mechanisms that might also couple optic flow detection with locomotion (Keller, Bonhoeffer & Hübener, 2012; Niell & Stryker, 2010). The conscious processing that takes place in Area V1 may become necessary for visually guided locomotion in cluttered, dynamic environments in order to avoid collisions with stationary and moving objects. That is, both the neural pathway that by-passes Area V1 and the neural pathway that passes through Area V1 potentially contribute to visually guided locomotion. Their relative contribution depends on the complexity of the environment to be navigated.

6.2 Effects of non-visual signals

Effects of non-visual signals on perceived optic flow have been indicated by a number of studies (e.g., Andersson et al. 1981; Pelah & Barlow, 1996; Warren et al. 2001; Thurrell & Pelah, 2002, 2005; Durgin et al. 2005; Tcheang et al. 2005). For locomotion, the non-visual signals may originate from the control and movement of the locomoting limbs (Lappe, 1997), as proprioceptive afferents, signals of spinal origin or associated corollary discharge signals (sometimes called reafferent or efference copy). Although such inputs to extrastriate regions associated with limb movement have not been identified, analogous modulation of optic flow neurons in MSTd by non-visual signals has been observed for pursuit eye movements (Newsome et al. 1988) and

vestibular signals (Duffy, 1998; Bremmer, et al, 2001; Gu et al, 2006; Fetsch, et al, 2007). The results of the current study suggest that non-visual locomotor-based signals, if present, are integrated with the detected optic flow in order to determine its perceived speed, and thereby signal the speed of locomotion (Pelah and Barlow, 1996). This could occur at or prior to extrastriate processing and operate without projections to, or feedback from, Area V1.

6.3 Motion detection mechanisms

The results obtained in this study are also relevant to identifying the kind of motion mechanism that is the basis for the detection of optic flow. As indicated earlier, it has been found that the discrimination of motion direction in GY's cortically blind hemifield, where object perception is severely impaired, is based on the detection of 1st-order motion energy; i.e., stimulus information entailing spatiotemporal changes in luminance rather than changes in shape (Azzopardi & Hock, 2011; Sperling & Lu, 1998; Hock & Nichols, 2013). The evidence in the current study for visuo-locomotor coupling in GY's cortically blind hemifield implies that the detection of locomotion-induced optic flow in GY's blind hemifield likewise entails the detection of motion energy. That is, in contrast with changes in the features of an object that determine both its shape and direction of motion, motion perception would be based on detected motion energy, which has been characterized as 'objectless' (Sperling & Lu, 1998; Hock & Nichols, 2011, 2013) because it provides a sense of motion without a sense of what it is in the environment that has moved (an apt characterization of optic flow perception).

In contrast with optic flow, the processing of object motion is thought to depend on the detection of changes in the features of the object (e.g., changes in edge contrast at the object's boundaries; Hock & Nichols, 2010; 2013)[Footnote 2]. In normal vision this would take place along a parallel neural pathway that passes through Area V1 en route to Area MT and other extrastriate areas, enabling conscious awareness of the object's shape and direction of motion (Lamme, 2001; Silvanto et al. 2005).

As we walk or run through a natural environment, the retinal optic flow created by our locomotion is vectorially combined with the independent retinal motion of objects in the environment. In light of the above evidence for differences in motion processing in the parallel pathways to Area MT (whether through or by-passing Area V1), it can be speculated that mutually inhibitory interactions among Area MT neurons (Snowden et al. 1991; Recanzone et al. 1997; Heeger et al. 1999; Thiele, Dobkins & Albright, 2000), some of which are motion energy sensitive and some of which are not (Krekelberg & Albright, 2005), could form the basis for discounting the optical effects of locomotion on the perceived direction of object motion. Interactions of "objectless' optic flow with non-visual signals would modulate optic flow speed, and remain essential for visually guiding the walkers' self-motion perception as they move through natural or altered environments (Pelah & Barlow, 1996).

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Footnotes

    1. Because the nested squares stimuli were so dim, it is unlikely that the results for stimuli presented in GY's blind field were due to light scatter into his sighted hemifield. This was confirmed by additional blocks of trials in which scatter from the cortically blind into the normally sighted visual field was masked by stimulating GY's normally sighted hemifield with a bright, 27.0 deg x 90.0 deg, field of uniform, 4.7 cd/m^2 light (displaced 0.5 deg from fixation). The high correlation between walking speed and optic flow speed confirmed that the locomotor speed-matching results obtained in GY's blind field were not due to leakage from light scatter into the sighted hemifield.

    2. Structure-from-motion stimuli that result in the perception of an object (e.g., dots on an otherwise transparent rotating sphere) are sometimes referred to as optic flow stimuli. However, our comments regarding object motion are concerned with translational motion relative to locomotion-induced optic flow, and not the internal motions that allow for the recovery of an object's shape.

    3. For the trials with gradually changing optic flow speed, walking speed was averaged between 4 and 6 secs into the 24 sec trial and the last 2 sec of the trial. For the trials with abruptly changing optic flow speed, walking speed was averaged between 3 and 5 secs into the 24 sec trial and the last 2 sec of the trial.

Figure Captions

Figure 1. Presentation of optic flow stimulus while test subject is walking on a treadmill. (a) Sketch of the testing apparatus. Note the absence of visual information in the region that would stimulate the macula and (in this case) the left hemifield. (b) Four optic flow speed values determined over a range of eccentricities, measured at the mid-hemifield location of the optic flow stimulus (27.8 deg, as indicated by the vertical broken line).

Figure 2. Results for Experiment 1: (a) Perceived optic flow speed as a function of walking speed for the expanding optic flow stimulus presented in (a) GY's normally sighted hemifield, (b) GY's cortically blind hemifield (block 1), and (c) GY's cortically blind hemifield (block 2).

Figure 3. Additional results for Experiment 1. (a) Verbal ratings on a four point scale for optic flow stimuli presented in either GY's normally sighted or cortically blind hemifield. Perceived speed as a function of walking speed for (b) a vertically drifting grating, and (c) a rotating cartwheel, both of which were presented only in GY's cortically blind hemifield.

Figure 4. Experiment 2. Walking speed matched to constant optic flow speeds for stimuli presented in GY's normally sighted and cortically blind hemifields. The six graphs vary according to the luminance of the frames of the expanding optic flow stimulus.

Figure 5. Single trials for GY walking to match time-varying optic flow speeds. The optic flow speeds either increased or decreased, and did so either gradually or abruptly