Enhanced optic flow speed discrimination while walking: Contextual tuning of visual coding

Frank H. Durgin and Krista Gigone

Swarthmore College

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Correspondence to:
Frank H. Durgin
Department of Psychology
Swarthmore College
500 College Avenue
Swarthmore, PA 19081

e-mail: fdurgin1@swarthmore.edu
phone: 610-328-8678
fax: 610-328-7814

Abstract

The authors test the hypothesis that long-term adaptation to the normal contingencies between walking and its multisensory consequences (including optic flow) leads to enhanced discrimination of appropriate visual speeds during self-motion. In Experiments 1 (task 1) and 2 a two-interval forced choice procedure was used to compare the perceived speed of a simulated visual flow field viewed while walking with the perceived speed of a flow field viewed while standing. Both experiments demonstrated subtractive reductions in apparent speed. In Experiments 1 and 3 discrimination thresholds were measured for optic flow speed while walking and while standing. Consistent with the optimal coding hypothesis, speed discrimination for visual speeds near walking speed was enhanced during walking. Reduced sensitivity was found for slower visual speeds. The multisensory context of walking alters the coding of optic flow in a way that enhances speed discrimination in the expected range of flow speeds.

Enhanced optic flow speed discrimination while walking

For most humans, walking is a common activity that is guided and controlled by multisensory spatial information (eg Sun Campos and Chan 2004). Walking produces a multitude of sensory signals (visual, vestibular, proprioceptive). These feedback signals, which can be used to estimate speed and distance of travel, are causally connected to motor activity, and are therefore highly correlated with one another. In this article we will consider the theory that adaptation to correlated patterns of information can produce coding advantages within a sensory channel. Specifically, we will show that the very act of walking produces a shift in visual coding that facilitates the discrimination of appropriate optic flow speeds. We suggest that enhanced coding can occur because the intercorrelation of sensory and motor signals in such a highly practiced activity provides an opportunity for intersensory tuning to occur, similar to unimodal contingent adaptation (Barlow 1990). Previously we have shown that the perceived speed of optic flow is reduced during normal walking, as well as during passive linear self-motion and treadmill walking (Durgin Gigone and Scott 2005) – reductions from normal walking are approximately the sum of the inertial and biomechanical component conditions. Here we argue that these speed reductions should be construed as adaptive coding shifts and show that the perceptual discrimination of optic flow speeds is enhanced for optic flow speeds that are near or higher than walking speed.

Adaptability is one of the hallmarks of biological perceptual systems, as illustrated by well-known visual aftereffects. One of the oldest known of these is the waterfall illusion (motion aftereffect), described by Aristotle (see Wade and Verstraten, 1998). A few minutes of staring at visual motion produces two effects: (1) reduction in the perceived speed of motion (e.g., Carlson 1962) and (2) subsequent perception of motion in the opposite direction when viewing a static image. Aftereffects are sometimes regarded as resulting from the fatigue of neurons, such as motion-selective units in area MT, but a number of findings have cast doubt on this view. Though they normally "decay" with time, aftereffects tend to be preserved during periods of visual inactivity (MacKay and MacKay 1975; Thompson and Movshon 1978; Wohlgemuth 1911). This seems inconsistent with fatigue. Moreover, aftereffects to expanding flow fields are reduced when accompanied by physical self-motion (L. Harris Morgan and Still 1981; Pelah and Boddy 1998; Wallach and Flaherty 1975), which also suggests a more complicated origin. Rather than being due to neural fatigue, aftereffects are more likely side-effects of highly functional mechanisms that normally tune or recalibrate perceptual systems (see Mather and J. Harris 1998 for a review. See also Dodwell and Humphrey 1990).

Functional theories of adaptation have proposed that more efficient coding can be promoted by the build-up of mutually inhibitory interactions between simultaneously activated neural units (Barlow 1990; Barlow and Foldiak 1989). Just as dark adaptation shifts the range in which discriminations of lightness may be made, it has been hypothesized that adaptation to visual motion, for example, might shift the zero-point for encoding motion. Indeed, enhanced perceptual discrimination of visual speeds near the adapting speed has been reported (Clifford and Wenderoth 1999). Similar enhancements of discrimination following adaptation have been reported for perceived contrast (Greenlee & Heitger 1988).

However, coding efficiency goes beyond adjusting a single perceptual dimension (Barlow 1990; Durgin and Proffitt 1996). Optimal coding schemes are particularly useful when they are sensitive to contingencies among sensory channels or between sensory and motor channels because this provides for more flexible tuning of perceptual systems that are embedded in a rich multisensory web of information. The presence of optic flow during forward self-motion is omnipresent in everyday experience. Thus, optimal coding theories predict that during self-motion the visual speed of appropriate flow should appear slower, consistent with a change in the zero-point. Durgin, Gigone and Scott (2005) demonstrated subtractive speed reduction for passive as well as active self-motion. More controversially, these schemes predict enhanced speed discrimination for visual speeds that correspond to the rate of travel.

What little evidence there is, however, has been used to argue that perception of visual speed during self-motion is actually impaired (Probst Krafczyk Brandt and Wist 1984; Wallach 1987; Wertheim 1994). This impairment has been attributed to the "suppression" of motion signals for the sake of perceived world stability. Although these results appear contrary to the optimal coding hypothesis, these earlier studies concerned the perception of object motion rather than of visual self-motion.

For the purpose of calibrating locomotor walking speed (eg Rieser Pick Ashmead and Garing 1995), it is important to discriminate visual speeds produced by walking. According to Barlow's (1990) model, this could be facilitated by subtractive inhibition of visual motion signals by concomitant self-motion information, such as, for example, motor signals of locomotion, proprioceptive information about the configuration of the body and vestibular and other inertial signals. Many previous studies have demonstrated inhibitory visuo-vestibular interactions during self-motion, but these findings are generally interpreted as evidence that the suppression of visual motion signals is designed to eliminate them (Dichgans and Brandt 1978; Brandt, Bartenstein, Janek and Dietrich 1998). Although some explanation must be given for apparent world stability during self-motion (Wallach 1987), the notion that visual motion signals ought to be eliminated runs counter to the idea that these same motion signals are used to infer self-motion (but see Wertheim 1994). For example, by manipulating a moveable room around a separately moveable cart, Lishman and Lee (1973) demonstrated visual dominance over vestibular signals in the perception of linear self-motion. This suggests that the visual perception of self-motion ought to be highly tuned (rather than suppressed) so that it may serve as effective feedback for motor control. Here we show that when judgments are made concerning the visual speed of the entire flow field, the functional predictions of the optimal coding theory are supported.

Barlow’s model (Barlow 1990; Barlow and Földiák 1989) of subtractive inhibition between correlated dimensions is expressed in Equation 1, in which perceived visual flow speed (Ψ_v), in this case, is proportional to the actual visual flow speed (V) minus a constant proportion (k) of another perceived dimension, such as walking speed (Ψ_w):

$$(1)\ \Psi_v = V - k\Psi_w$$

Figure 1 illustrates how the model, when applied to correlated values (such as visual flow speed and locomotor speed, Panel A), can decorrelate the two dimensions. Most important for the present context, if we consider that coding precision depends both on the bandwidth of a code (the number of divisions it can make) and on the range of values the code must be applied to, it can be seen that coding advantages might be achieved by reducing the range of values that need to be considered, as occurs in Panel B, where the model is applied with $k = 0.5$. When the same coding space can be applied to a smaller range, one can encode values with greater precision. This is the equivalent of shifting the coding space with locomotor speed, as illustrated in Panel C. Barlow (1990) emphasized that the conjoint coding space of correlated dimensions is better filled by applying his model to both correlated dimensions (Panel D).

Figure 1 about here.

To test the optimal coding hypothesis, we conducted three experiments in which observers walked or stood in a real environment and made judgments about the apparent speed of visual flow presented to them in a virtual environment. Note that much as one may be aware of the darkness cast by a shadow across a surface while also seeing the surface as intrinsically uniform in lightness, awareness of the optic flow rate produced by self-motion can occur alongside apparent world stability. In the experiments reported here, perceptual judgments were made with respect to the apparent speed of optic flow, not of the world, though our conclusions regarding precision do not depend on this distinction.

We emphasize that the speed of optic flow in these experiments was not directly tied to the speed of walking – though the speeds presented were meant to include normal walking speeds. Thus, the information provided by the act of walking did not help to specify the actual visual speeds. Rather, the contribution of non-visual information was limited, in our theoretical terms, to generating an automatic shift in the perceptual coding space for optic flow, by predicting (based on normal experience) a general range of expected visual speeds. As we will show below, when the presented speeds were well below that range, visual speed discrimination was compromised rather than enhanced by walking. This is consistent with the idea that subtraction adds estimator noise that cannot always be compensated for by the coding benefits – especially when the signal is artificially reduced. Subtraction is not necessarily advantageous for lower-than-expected speeds, because the added variance (from estimates of locomotor speed) would be proportionally greater compared to the magnitude of the signal.

Experiment 1: Flow speed perception and discrimination while walking

To test the idea that speed discrimination would be enhanced during walking (for appropriate flow speeds) we conducted a two-part experiment. In the first part, we presented one visual speed during a period of walking and a second during standing and asked observers to judge which visual speed seemed faster. Observers were instructed concerning the distinction between visual speed and apparent world speed and asked to report only on visual speed. We expected to find evidence supporting the conclusion of Durgin et al. (2005) that flow speeds while walking were reduced by a constant difference (proportional to walking speed).

In the second part of the experiment, the same participants were asked to make comparisons between pairs of visual speeds presented in the same locomotor state: both speeds were viewed while standing or while walking. This allowed us to assess the effect of locomotor state on visual speed discrimination. We expected to find evidence of enhanced speed discrimination during walking for visual speeds near walking speed.

Methods

Participants: Ten undergraduate students at Swarthmore College who were unaware of the experimental hypotheses were paid to participate.

Apparatus and Display: The visual speed stimuli were presented stereoscopically in a V8 head-mounted display (HMD) with a 60° diagonal field of view (approx. 38 degrees vertical and 50 degrees horizontal). The virtual environment consisted of a hallway 2 m wide and 2.5 m high viewed from eye-height in stereo rendered and displayed at 60 Hz with 640- x 480-pixel resolution. To be naturalistic, the display was immersive and compensated for all head-movements except for translations along the axis of motion. A HiBall optical head-tracker provided sub-mm precision at 120 Hz. Total display lag was about 38 ms. To facilitate accurate flow speed scaling, the virtual environment included a textured ground plane as well as textured walls and ceiling during the presentation of motion stimuli. Between visual speed displays, a gray, featureless hallway provided visual guidance so that gaze and walking could be oriented toward the distantly visible end of the virtual hallway without specifying a visual speed. The physical space in which the experiment took place was a hallway (2.4 m wide) of which 15 meters were instrumented for head-tracking.

Speed Comparison Task: On each trial, participants first walked forward at a normal speed and, while walking, saw a visual flow field for 2.5 seconds (the hallway texture was turned on once full walking speed was reached, and moved at a fixed rate of speed along the main hallway axis). They then stopped and saw a second flow field for 2.5 seconds and judged whether the second flow field appeared faster or slower than the first. (Pilot testing showed that presenting the standard in the first interval produced comparisons dominated by the global mean speed.) We used this two-interval forced-choice (2IFC) task in a staircase procedure to assess the speeds presented during walking that subjectively matched speeds of 25, 75 and 125 cm/s (the standards) presented while standing. This range bracketed normal walking speed (which averaged 110 cm/s in the experiment). Thirty judgments were made by each of the participants at each of the three standard speeds. For each speed, three staircases were sampled once in each of ten blocks of trials. Staircases started with speeds (centered at about half of the expected subtraction value) that were -24, +18, and +60 cm/s relative to each standard (M = +18 cm/s). Step size after each judgment was 18 cm/s up or down. Each staircase produced 10 trials. This procedure took about 25 minutes and was followed by a break.

Speed Discrimination Task: During the break, a new task was explained to the participants. In this task, two visual motion intervals were presented while the participant walked or while the participant stood. The same range of visual speeds was used as in the first task and standing and walking trials were alternated. Staircase methods were again used, but this time to estimate discrimination thresholds at each of the three standard speeds while standing and while walking. That is, participants alternated between comparing two visual speeds while standing and two visual speeds while walking. The participants again made 2IFC judgments, comparing the second interval to the first, for speeds near 25, 75 and 125 cm/s. Motion duration was between 1.25 and 1.5 s in each interval. Each participant made a total of 120 judgments, consisting of 20 judgments of each of the three relevant speeds while walking and another 20 while standing still. The two staircases for each cell started at –40% or +40% of the standard speed and the step size was 15% of the standard. Each staircase was sampled once in each of ten blocks of trials. Limited data were collected for each participant so as to minimize adaptation to the experience of the experiment itself, so we depended on having multiple participants to detect reliable differences. Because the participants had recently completed Experiment 1, they were practiced at making speed comparisons in the range used. The procedure took about 25 minutes.

Results

The results for the two tasks are shown in Figure 2. As expected the speed comparison task in part 1 revealed a constant subtraction across visual speeds during walking. Most importantly, in part 2, discrimination thresholds for speeds near walking speed were enhanced by walking, while those for lower speeds were compromised. Note that speed-specific improvement suggests that enhanced performance is not simply due to visual effects of bob and sway[1]. Details of the analyses are presented separately for each task below.

Figure 2 about here.

Speed Comparison Task. Points of subjective equality (PSEs) were estimated for each speed for each participant using a logistic function. Averages of these PSEs are shown in the left panel of Figure 2 (a sample logistic fit is inset). As is evident from the figure, the amount of simulated speed added during walking was approximately constant across all visual speeds, though the judgments for the lowest speeds were quite variable (perhaps because perceived speeds while walking were so often near zero). Overall the average visual subtraction (i.e. the average simulated speed increment during walking) was 51 cm/s. That is, a visual speed of about 176 cm/s viewed while walking looked equal in speed to a visual speed of 125 cm/s while standing still. This represents a subtraction by 46% of the average walking speed (110 cm/s).

Speed Discrimination Task. Logistic functions were used to estimate discrimination thresholds for each standard speed in each locomotor state. Averages of these 75% discrimination thresholds are shown in the right panel of Figure 2. Consistent with the optimal coding hypothesis, optic flow speed discrimination was significantly better while walking than while standing for the visual speed nearest walking speed (i.e. 125 cm/s), $t(9) = 2.39$, $p < .05$, whereas low visual speeds (e.g. 25 cm/s) became quite difficult to discriminate during walking. Average discrimination thresholds during walking for these low visual speeds were significantly elevated relative to performance while standing, $t(9) = 2.53$, $p < .05$.

Discussion

Previous research has suggested that visual speeds appear reduced during self-motion Gigone and Scott 2005; Pavard and Berthoz 1977; Thurrell Pelah and Distler 1998; Wallach and Flaherty 1975). Durgin, Gigone and Scott used the method of magnitude estimation to show that speed reduction was subtractive and that the amount of subtraction was proportional to walking speed (see also Thurrell et al. 1998). Using a two-interval forced-choice method, we have found that an average of 51 cm/s or 46% of walking speed had to be added to the visual display during walking for it to appear equal to a visual speed viewed while standing. This constant subtraction is exactly the characteristic predicted by contingent recoding according to Barlow's model as we have extended it to the case of multisensory perception. The current value is fairly similar to the 37% subtraction found by Durgin, Gigone and Scott with similar displays.

It has previously been argued that reduced speed perception during self-motion is accompanied by (or caused by) poorer speed discrimination during self-motion. However, optimal coding theory predicts that the subtraction found in the first part of Experiment 1, though detrimental to the discrimination of lower-than expected visual speeds, has the function of enhancing speed discrimination at speeds near walking speed. These speed-specific predictions were supported by the present results. These results represent the first evidence of enhanced speed discrimination in vision produced by the multisensory context of walking.

Experiments 2 and 3: Between-subjects replication

It is possible that the results of Experiments 1, although consistent with our theoretical hypotheses, were due to range-specific adaptation to the speeds shown (Clifford and Wenderoth 1999). Perhaps by using speeds that were centered on 75 cm/s we enhanced discrimination of speeds that had the visual appearance of 75 cm/s. To address this possibility we conducted two new experiments in which we varied standard speed between subjects. In addition, a larger range of speeds was tested and more data were collected for each psychophysical estimate. In fact, the results were similar to those of Experiment 1.

Participants

Participants in Experiments 2 and 3 were 80 undergraduate students who were paid for their participation. Fifty were tested in a speed comparison task (Experiment 2) and 30 were tested in a speed discrimination task (Experiment 3). In all cases only a single standard speed was employed for each participant. All conditions were approximately balanced for sex of participant.

Apparatus

The same apparatus was used as in Experiment 1 except that a higher-resolution HMD, (nVisor SX), with 1280 x 1024 pixels was used for these experiments. The FOV (60 deg diagonal -- approximately 40 degrees vertical and 49 degrees horizontal) was similar to that in Experiments 1 and was refreshed with the same frequency (60 Hz). The virtual environment was the same and was again viewed stereoscopically.

Experiment 2: Speed comparison

Five standard speeds (25, 75, 125, 175 and 225 cm/s) were tested (with 10 participants each). For half the participants, the standard speed was presented in the first interval while they stood still, and the variable speed was presented in the second interval while they walked. For the other half, subjects walked and saw the variable interval first and then stood while watching the standard (as in Experiment 1). There were 6 practice trials followed by 48 analyzed trials used to compute the PSE between walking and standing. Six staircases were used, with starting values (centered around half the expected subtraction value) that were –24, -12, +18, +36, +66, and +78 cm/s relative to the standard speed (M = +27 cm/s); step size was 18 cm/s. The procedure took about 20 minutes.

Results and Discussion

Although all 50 participants were encouraged to walk rapidly, head tracking records indicated that participants in the slowest and very-fast visual speed conditions (25, 175, and 225 cm/s) walked more slowly (118, 115, 117 cm/s) than those in the 75 and 125 cm/s visual speed conditions (135 and 139 cm/s). These last speeds are somewhat more normal for instructions to walk rapidly (Durgin Reed and Tigue 2006), suggesting that walking was more normal when visual speeds were appropriate to walking. Because Durgin et al. (2005) showed that subtraction was proportional to walking speed, PSEs were divided by the average walking speed for each participant to compensate for differences in walking speed. These measures of proportional speed subtraction, shown in the left panel of Figure 3, were analyzed using an ANOVA with speed (5 levels) and order (walk first or stand first) as between-subject variables. Consistent with the basic subtraction model, no differences were found by speed or order. That is, speed subtraction was proportional to walking speed, but largely independent of visual speed. There was a trend for greater proportional subtraction at visual speeds near normal walking speeds. Overall, the average level of subtraction was by 28% of walking speed, though it was 37% for the visual speed of 125 cm/s. It is possible that more immersive speeds promoted greater multisensory/motor integration.

Figure 3 about here.

Experiment 3: Speed discrimination

The speed discrimination task was similar to that of Experiment 1. Four standard speeds (75, 125, 175, and 225 cm/s) were tested (with 7 or 8 participants each). The low speed of the previous experiment (25 cm/s) was not used because of the difficulty of making speed discriminations for flow speeds that appeared to be zero, while walking. There were 28 practice trials (alternating between standing trials and walking trials), followed by 96 trials for computing speed discrimination thresholds while walking and while standing (48 trials each). Staircases started at –28%, +28%, or equal to the standard; step size was 12% of the standard. Six staircases each for walking and for standing were sampled twice per block for five blocks, with the first block considered practice. The procedure took about 30 minutes.

Results and Discussion

Average walking speed did not differ reliably as a function of visual speed in this experiment, and averaged 124 cm/s overall. Discrimination thresholds are plotted in the right panel of Figure 3 (a sample logistic fit is inset). For 3 of the 4 speed conditions these thresholds differed by locomotor state. For those who made judgments of the lowest visual speed (75 cm/s), performance was better when standing than when walking, $t(7) = 2.03$, $p < .05$, one-tailed, whereas for those who judged the highest visual speed

(225 cm/s) and for those who judged the visual speed nearest walking speed (125 cm/s), discrimination was better while walking then when standing, $t(6) = 3.01$, $p < .05$; $t(7) = 2.36$, $p < .05$, one-tailed[2]. The data for the two speeds that were used in both discrimination experiments (75 cm/s and 125 cm/s) closely replicate the discrimination values found in Experiment 1, indicating that the earlier results were not artifacts of the speed range used.

General Discussion

Our results are consistent with the thesis that visual motion signals associated with self-motion are adaptively modified by the multisensory action context in which they occur. Whereas previous theorists have emphasized loss of visual speed information while moving, the present study suggests a facilitative role for speed subtraction in the coding of visual flow. We suggest that coding advantages result from long-term adaptation to multisensory correlations during walking. The primary goal of such perceptual tuning is not error correction or "calibration" in the normal sense (Barlow 1990; Durgin 1996; Durgin and Proffitt 1996; Durgin Gigone and Scott 2005). Rather, it is the multisensory fitting of perceptual coding space to sensory experience. When correlations exist in experience, such as those among self-motion signals, the various signals may become mutually inhibiting, thereby enhancing the allocation of their various coding scales in the conjoint estimation of, in this case, self-motion.

In an optimized system, the amount of subtraction ought to reflect the precision of the two estimators. If a coding shift is to be advantageous, the estimation noise added by the subtraction process must be compensated for by the advantages accorded by the reduced coding range. For slower-than-appropriate visual speeds this is not guaranteed. The fact that discrimination for visual speeds of 75 cm/s (60% of normal walking speed) was compromised by walking in Experiment 3 (and trended the same way in Experiment 1) is consistent with the model and seems to rule out certain alternative explanations regarding how walking might contribute to the enhancement of discrimination (such as motion parallax added by the bob and sway of the head).

The results of Experiment 1 suggested that visual speed was reduced by an amount corresponding to about 46% of walking speed. This finding was replicated in a between-subject design in Experiment 2, with subtraction of 37% of walking speed for visual speeds near walking speed. Based on optimal coding theory, we predicted that speed discrimination should be enhanced for visual speeds at or above walking speed while the discrimination of lower speeds would suffer. These two predictions were upheld by the results of Experiments 1 and 3.

Perceptuo-motor recalibration can be rapid. Pelah and Barlow (1996) showed that the perceived speed of optic flow was increased during walking that occurred following extended adaptation to (stationary) treadmill running with open eyes – a finding we can now reinterpret as a release from subtractive inhibition following adaptation to a breakdown of the normal contingencies. Adaptation to treadmill locomotion with or without visual feedback also produces shifts in locomotor estimates of the speed of self-motion (Durgin Fox and Kim 2003; Durgin Pelah et al. 2005). After treadmill locomotion, attempts to walk to a visually-previewed target without visual feedback will result in overshooting the target, as if locomotor speed were underestimated. Normally, people are fairly accurate at this kind of visually-directed walking task (Loomis Da Silva

Fujita and Fukusima 1992; Rieser Ashmead Talor and Youngquist 1990; Sun Campos Young Chan and Ellard 2004). This suggests that the locomotor system is normally well-calibrated. Visual feedback may be used to tune and supplement locomotor estimates – though the recalibration of motor/kinesthetic estimates appears to be based on the totality of self-motion information available (Durgin and Pelah 1999; Durgin Pelah et al 2005).

We have shown that discrimination thresholds for appropriate visual speeds are enhanced during walking. This enhanced sensitivity would be particularly useful for detecting discrepancies between intended and achieved actions (Durgin Fox Schaffer and Whitaker 2005). Although biomechanical information may dominate non-visual self-motion perception (Mittelstaedt and Mittelstadt 2001), it is worth noting that biomechanical activity alone (i.e., walking on a treadmill) produces less visual speed subtraction than does walking on solid ground (Durgin Gigone and Scott 2005). Normal walking represents a special case of an over-learned activity for which full multisensory optimization might be expected. Locomotion may therefore provide a particularly advantageous situation for measuring enhancements of visual sensitivity from other senses. Nonetheless, these functional advantages of multisensory coding probably apply elsewhere.

References

Barlow H B, 1990 "A theory about the functional role and synaptic mechanism of visual aftereffects", in *Vision: Coding and efficiency* Ed. C Blakemore (Cambridge: Cambridge University Press) pp 363–375

Barlow H B, Földiák P, 1989 "Adaptation and decorrelation in the cortex", in *The computing neuron* Eds. R M Durbin, C Miall, G J Mitchison (Wokingham: Addison Wesley) pp 54–72

Brandt T, Bartenstein P, Janek A, Dietrich M, 1998 "Reciprocal inhibitory visual-vestibular interaction: Visual motion stimulation deactivates the parieto-insular vestibular cortex" *Brain* **121** 1749–1758

Carlson V R, 1962 "Adaptation in the perception of visual velocity" *Journal of Experimental Psychology* **64** 192–197

Clifford C W G, Wenderoth P, 1999 "Adaptation to temporal modulation can enhance differential speed sensitivity" *Vision Research* **39** 4324–4332

Dichgans J, Brandt T, 1978 "Visual-vestibular interaction: Effects on self-motion perception and postural control", in *Handbook of sensory physiology Vol 8*: *Perception* Eds. R Held, H W Leibowitz, H-L Teuber (Berlin: Springer-Verlag) pp 755–804

Dodwell P C, Humphrey G K, 1990 "A functional theory of the McCollough effect" *Psychological Review* **97** 78-89

Durgin F H, 1996 "Visual aftereffect of texture density contingent on color of frame" *Perception & Psychophysics* **58** 207-233

Durgin F H, Fox L F, Schaffer E, Whitaker R, 2005 "The perception of linear self-motion", in *Human Vision and Electronic Imaging X, proceedings of SPIE-IS&T Electronic Imaging SPIE Vol 5666* Eds. B E Rogowitz, T N Pappas, S J Daly pp 503-514

Durgin F H, Fox L F, Kim D H, 2003 "Not letting the left leg know what the right leg is doing: Limb-specific locomotor adaptation to sensory-cue conflict", *Psychological Science* **16** 567-572

Durgin F H, Gigone K, Scott R, 2005 "Perception of visual speed while moving", *Journal of Experimental Psychology: Human Perception and Performance* **31** 339-353

Durgin F H, Pelah A, 1999 "Visuomotor adaptation without vision?" *Experimental Brain Research* **127** 12-18

Durgin F H, Pelah A, Fox L F, Lewis J Y, Kane R, Walley K A, 2005 "Self-motion perception during locomotor recalibration: More than meets the eye" *Journal of Experimental Psychology: Human Perception and Performance* **31** 398-419

Durgin F H, Proffitt D R, 1996 "Visual learning in the perception of texture: Simple and contingent effects of texture density" *Spatial Vision* **9** 423-474

Durgin F H, Reed C, Tigue C, 2007 "Step frequency and the perceived speed of self-motion" *Transactions in Applied Perception*

Greenlee M W, Heitger F, 1988 "The functional role of contrast adaptation" *Vision Research* **28** 791-797

Harris L R, Morgan M J, Still A W, 1981 "Moving and the motion after-effect" *Nature* **293** 139–141

Lishman J R, Lee D N, 1973 "The autonomy of visual kinaesthesis" *Perception* **2** 287-194

Loomis J M, Da Silva J A, Fujita N, Fukusima S S, 1992 "Visual space perception and visually directed action" *Journal of Experimental Psychology: Human Perception and Performance* **18** 906-921

MacKay D M, MacKay V, 1975 "What causes decay of pattern-contingent chromatic aftereffects?" *Vision Research* **15** 462-464

Mather G, Harris J, 1998 "Theoretical models of the motion aftereffect", in *The motion aftereffect: a modern perspective* Eds. G Mather, F Verstraten, S Anstis (Cambridge: MIT Press) pp 157-185

Mittelstaedt M-L, Mittelstaedt H, 2001 "Idiothetic navigation in humans: Estimations of path length" *Experimental Brain Research* **139** 318-332

Pavard B, Berthoz A, 1977 "Linear acceleration modifies the perceived velocity of a moving visual scene" *Perception* **6** 529–540

Pelah A, Barlow H B, 1996 "Visual illusion from running" *Nature* **381** 283

Pelah A, Boddy A, 1998 "Adaptive modulation of the motion after-effect by walking", [Abstract] *Journal of Physiology (London)* **506P** 111P–112P

Probst T, Krafczyk S, Brandt T, Wist E R, 1984 "Interaction between perceived self-motion and object-motion impairs vehicle guidance" *Science* **225** 536–538

Rieser J J, Ashmead D H, Talor C R, Youngquist G A, 1990 "Visual perception and the guidance of locomotion without vision to previously seen targets" *Perception* **19** 675-689

Rieser J J, Pick H L Jr, Ashmead D, Garing A, 1995 "Calibration of human locomotion and models of perceptual-motor organization" *Journal of Experimental Psychology: Human Perception and Performance* **21** 480-497

Sun H J, Campos J L, Chan G S, 2004 "Multisensory integration in the estimation of relative path length" *Experimental Brain Research* **154** 246-254

Sun H J, Campos J L, Young M, Chan G S, Ellard C G, 2004 "The contributions of static visual cues nonvisual cues and optic flow in distance estimation" *Perception* **33** 49-65

Thompson P G and Movshon J A, 1978 "Storage of spatially specific threshold elevation" *Perception* **7** 65-73

Thurrell A E I, Pelah A, Distler H K, 1998 "The influence of non-visual signals of walking on the perceived speed of optic flow" [Abstract] *Perception* **27** 147–148

Wade N, Verstraten F, 1998 "Introduction and historical overview", in *The motion aftereffect: a modern perspective* Eds. G Mather, F Verstraten, S Anstis (Cambridge: MIT Press) pp 1-24

Wallach H, 1987 "Perceiving a stable environment when one moves" *Annual Review of Psychology* **38** 1–27

Wallach H, Flaherty E W, 1975 "A compensation for field expansion caused by moving forward" *Perception & Psychophysics* **17** 445–449

Wertheim A H, 1994 "Motion perception during self-motion: The direct versus inferential controversy revisited" *Behavioral and Brain Sciences* **17** 293-355

Wohlgemuth A, 1911 "On the after-effect of seen movement" *British Journal of Psychology Monograph Supplement* **1** 1-117

Footnotes

1. Note also that Durgin et al. (2005 experiments 2 and 8) found that speed subtraction did not result from simply adding virtual bob and sway to standing conditions. Moreover Pelah and Boddy (1998) measured speed reduction on a treadmill with the head immobilized with a bite bar.

2. Although the "significance" of the result for 125 cm/s would not survive conservative Bonferroni corrections for multiple tests, this is a replication of a result of Experiment 1.

Author Notes

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Figure Captions

Figure 1. How Barlow’s model works. Panel A depicts the correlation to be expected between visual flow speed and locomotor speed. Panel B depicts the result of applying Equation 1 to the points in Panel A, reducing the range of speeds to be coded, thus allowing for finer distinctions with the same coding bandwidth. This is equivalent to dynamically moving the coding space for visual flow speed as function of locomotor speed (Panel C). Barlow (1990) emphasized that adaptive decorrelation spreads the data more evenly over the conjoint coding space (Panel D).

Figure 2. Results of Experiment 1. Left figure shows speed subtraction values (±SE) based on speed comparisons between standing and walking. Right figure represents mean discrimination thresholds (±SE) for the same participants when both intervals were viewed in the same locomotor state. Inset graphs show sample fits for one participant.

Figure 3. Results of Experiments 2 (left) and 3 (right). Values shown at left represent the mean speed subtraction value (±SE) expressed as a proportion of walking speed (25 – 225 cm/s; darker bars represent faster standard speeds). Each bar represents the data of five participants. At right are plotted discrimination thresholds (±SE) for optic flow speeds viewed while walking or while standing, where each pair of points represents data from 7 or 8 participants. For reference, lines representing Weber Fractions of 9% and of 6.5% are shown. Insets in each graph shows sample fits.

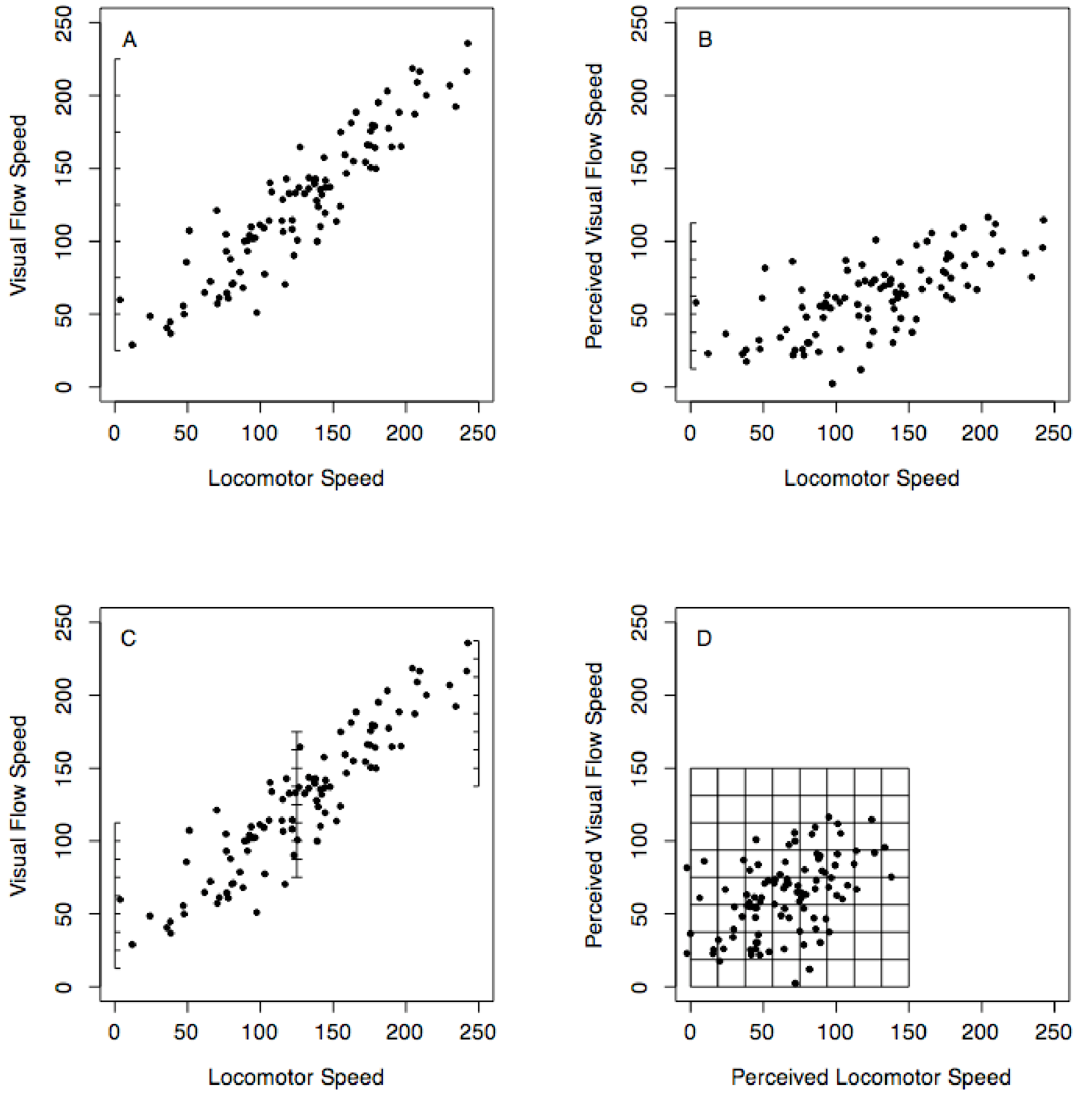
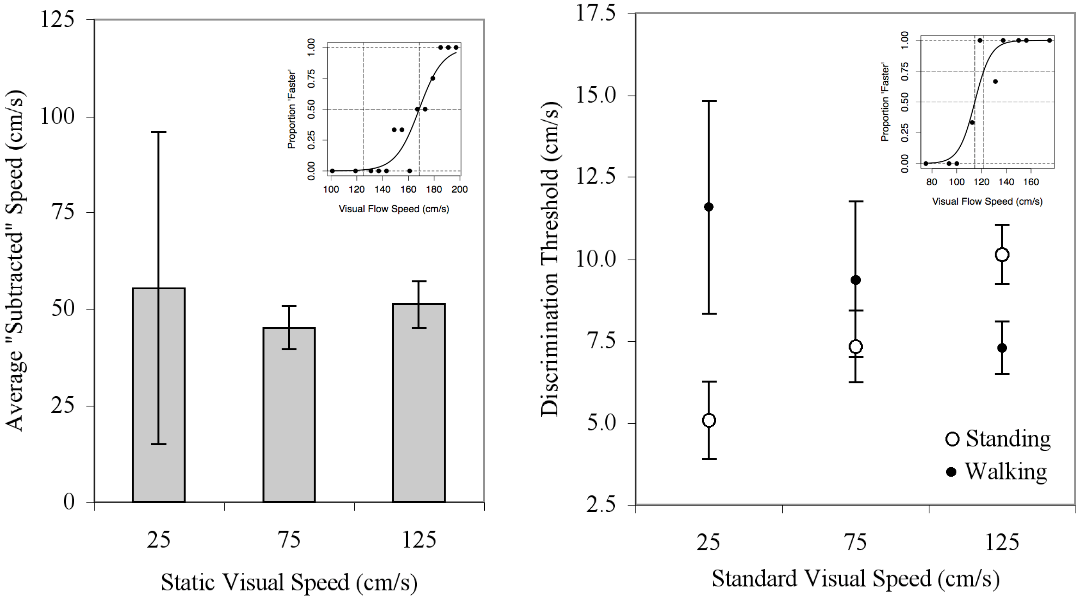

A
B
C
D
Visual Flow Speed
Perceived Visual Flow Speed
Locomotor Speed
Perceived Locomotor Speed
0
50
100
150
200
250

Figure 1



125
100
75
50
25
0
Average "Subtracted" Speed (cm/s)
25
75
125
Static Visual Speed (cm/s)
Proportion 'Faster'
0.00
0.25
0.50
0.75
1.00
100
120
140
160
180
200
Visual Flow Speed (cm/s)
17.5
15.0
12.5
10.0
7.5
5.0
2.5
Discrimination Threshold (cm/s)
25
75
125
Standard Visual Speed (cm/s)
○ Standing
● Walking
Proportion 'Faster'
0.00
0.25
0.50
0.75
1.00
80
100
120
140
160
Visual Flow Speed (cm/s)

Figure 2

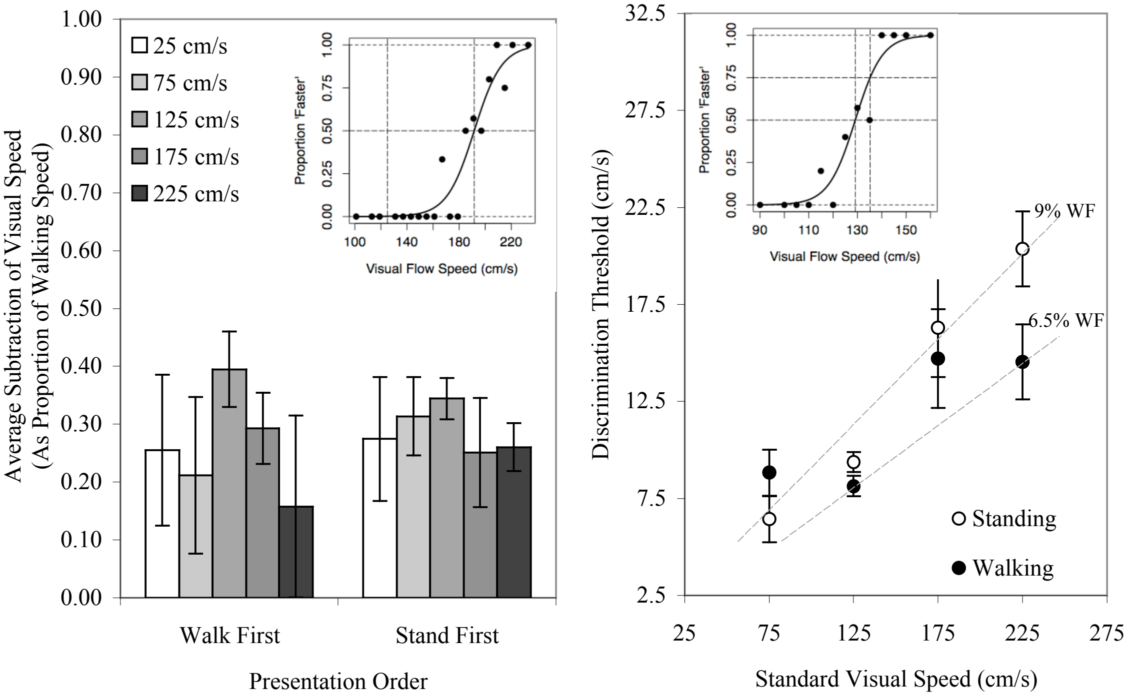

1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Average Subtraction of Visual Speed
(As Proportion of Walking Speed)
25 cm/s
75 cm/s
125 cm/s
175 cm/s
225 cm/s
Proportion 'Faster'
0.00
0.25
0.50
0.75
1.00
100
140
180
220
Visual Flow Speed (cm/s)
Walk First
Stand First
Presentation Order
32.5
27.5
22.5
17.5
12.5
7.5
2.5
Discrimination Threshold (cm/s)
Proportion 'Faster'
0.00
0.25
0.50
0.75
1.00
90
110
130
150
Visual Flow Speed (cm/s)
9% WF
6.5% WF
Standing
Walking
25
75
125
175
225
275
Standard Visual Speed (cm/s)

Figure 3