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Frank H. Durgin

Swarthmore College, fdurgin1@swarthmore.edu

Krista Marie Gigone , '04

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Frank H. Durgin and Krista Marie Gigone , '04. (2007). "Enhanced Optic Flow Speed Discrimination While Walking: Contextual Tuning Of Visual Coding". *Perception*. Volume 36, Issue 10. 1465-1475. DOI: 10.1068/p5845

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

Frank H Durgin, Krista Gigone

Department of Psychology, Swarthmore College, 500 College Avenue, Swarthmore, PA 19081, USA;
e-mail: fdurgin1@swarthmore.edu

Received 12 October 2006, in revised form 4 April 2007

Abstract. We tested 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.

1 Introduction

For most humans, walking is a common activity that is guided and controlled by multisensory spatial information (eg Sun et al 2004a). 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. Here, we consider the theory that adaptation to correlated patterns of information can produce coding advantages within a sensory channel. Specifically, we 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 et al 2005b)—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: (i) reduction in the perceived speed of motion (eg Carlson 1962) and (ii) 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; Wohlgenuth 1911).

This seems inconsistent with fatigue. Moreover, aftereffects to expanding flow fields are reduced when accompanied by physical self-motion (L Harris et al 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 Földiák 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 and 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 et al (2005b) 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 et al 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 et al 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 (Brandt et al 1998; Dichgans and Brandt 1978). 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):

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

Figure 1 illustrates how the model, when applied to correlated values [such as visual flow speed and locomotor speed (figure 1a)], 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 (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 (c). Barlow (1990) emphasized that the conjoint coding space of correlated dimensions is better filled by applying his model to both correlated dimensions (d).

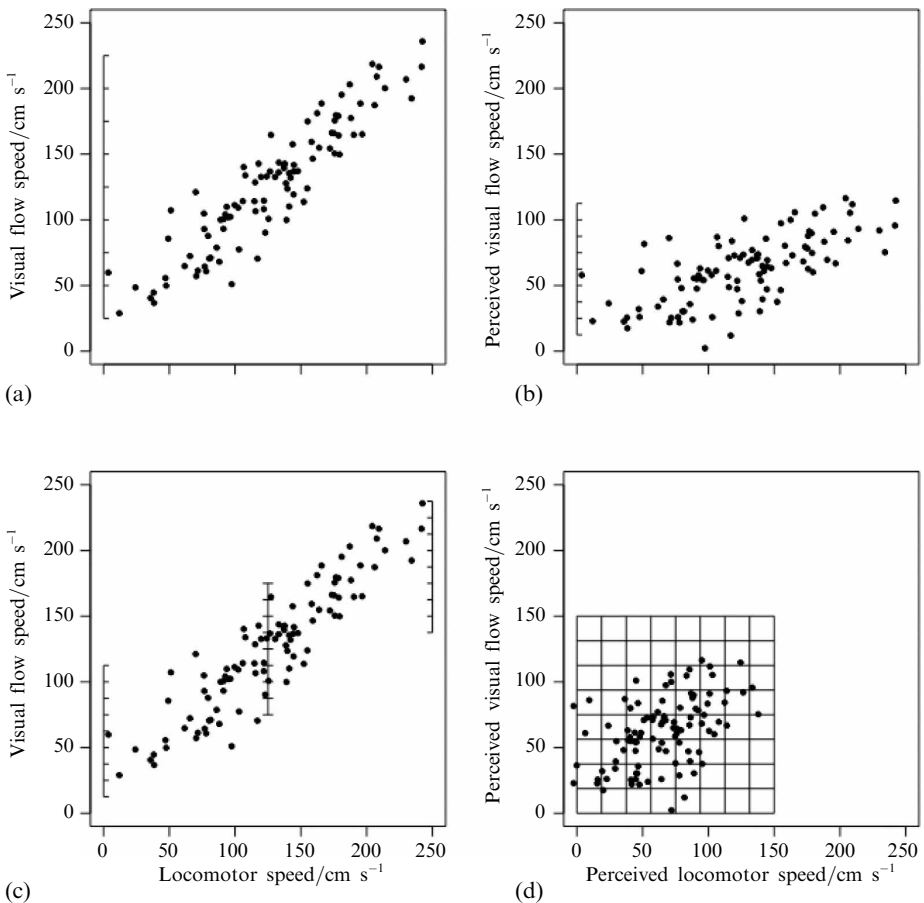


Figure 1. How Barlow's model works. (a) The correlation to be expected between visual flow speed and locomotor speed. (b) The result of applying equation (1) to the points in (a), reducing the range of speeds to be coded, thus allowing for finer distinctions with the same coding bandwidth. This is equivalent to dynamically moving the coding space for visual flow speed as function of locomotor speed (c). Barlow (1990) emphasized that adaptive decorrelation spreads the data more evenly over the conjoint coding space (d).

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 (on the basis of normal experience) a general range of expected visual speeds. As we will show below, when the presented speeds are well below that range, visual speed discrimination was impaired 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.

2 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 (2005b) 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.

2.1 Methods

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

2.1.2 Apparatus and display. The visual speed stimuli were presented stereoscopically in a V8 head-mounted display (HMD) with a 60 deg diagonal field of view (~ 38 deg vertical and ~ 50 deg 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 640×480 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 submillimeter 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 m were instrumented for head tracking.

2.1.3 *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 s (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 s 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⁻¹ (the standards) presented while standing. This range bracketed normal walking speed (which averaged 110 cm s⁻¹ 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⁻¹ relative to each standard (mean = +18 cm s⁻¹). Step size after each judgment was 18 cm s⁻¹ up or down. Each staircase produced 10 trials. This procedure took about 25 min and was followed by a break.

2.1.4 *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⁻¹. 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 min.

2.2 *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 impaired. 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.

⁽¹⁾Note also that Durgin et al (2005b, 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.

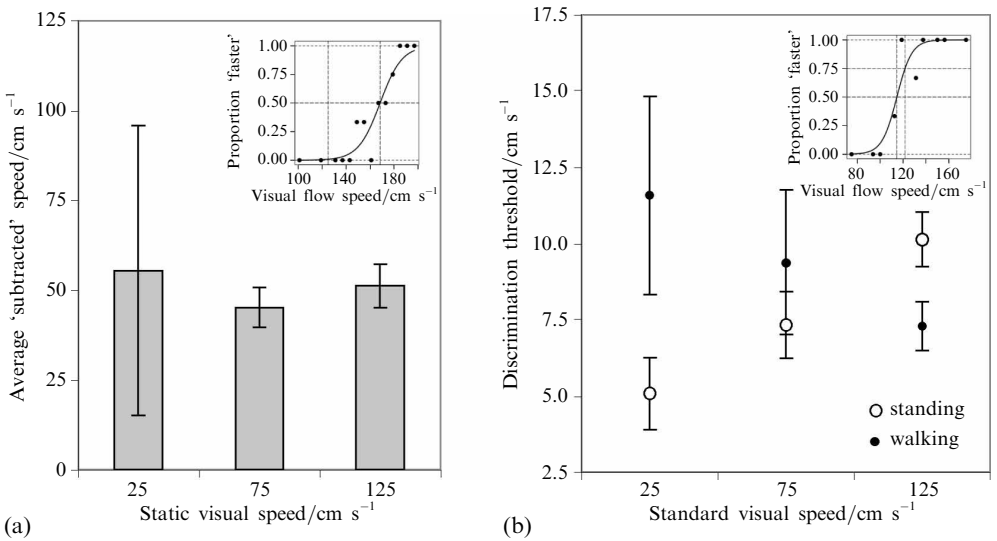


Figure 2. Results of experiment 1. (a) Speed subtraction values (\pm SE) based on speed comparisons between standing and walking. (b) Mean discrimination thresholds (\pm SE) for the same participants when both intervals were viewed in the same locomotor state. Inset graphs show sample fits for one participant.

2.2.1 Speed comparison task. Points of subjective equality (PSEs) were estimated for each speed for each participant by using a logistic function. Averages of these PSEs are shown in figure 2a (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 (ie the average simulated speed increment during walking) was 51 cm s^{-1} . That is, a visual speed of about 176 cm s^{-1} viewed while walking looked equal in speed to a visual speed of 125 cm s^{-1} while standing still. This represents a subtraction by 46% of the average walking speed (110 cm s^{-1}).

2.2.2 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 figure 2b. 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 (ie 125 cm s^{-1}) ($t_9 = 2.39$, $p < 0.05$), whereas low visual speeds (eg 25 cm s^{-1}) became quite difficult to discriminate during walking. Average discrimination thresholds during walking for these low visual speeds were significantly elevated over the performance while standing ($t_9 = 2.53$, $p < 0.05$).

2.3 Discussion

Previous research has suggested that visual speeds appear reduced during self-motion (Durgin et al 2005b; Pavard and Berthoz 1977; Thurrell et al 1998; Wallach and Flaherty 1975). Durgin et al (2005b) 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 2IFC method, we have found that an average of 51 cm s^{-1} 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 et al (2005b) 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 multi-sensory context of walking.

3 Experiments 2 and 3. Between-subjects replication

It is possible that the results of experiment 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^{-1} we enhanced discrimination of speeds that had the visual appearance of 75 cm s^{-1} . 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.

3.1 Method

3.1.1 *Participants.* Participants in experiments 2 and 3 were eighty undergraduate students who were paid for their participation. Fifty were tested in a speed comparison task (experiment 2) and thirty 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.

3.1.2 *Apparatus.* The same apparatus was used as in experiment 1 except that a higher-resolution HMD (nVisor SX), with 1280×1024 pixel resolution was used for these experiments. The FOV (60 deg diagonal: ~ 40 deg vertical and ~ 49 deg horizontal) was similar to that in experiment 1 and was refreshed with the same frequency (60 Hz). The virtual environment was the same and was again viewed stereoscopically.

3.2 Experiment 2. Speed comparison

Five standard speeds (25, 75, 125, 175, and 225 cm s^{-1}) were tested (with ten 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 matching 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 $+78 \text{ cm s}^{-1}$ relative to the standard speed (mean = $+27 \text{ cm s}^{-1}$); step size was 18 cm s^{-1} . The procedure took about 20 min.

3.2.1 *Results and discussion.* Although all fifty 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^{-1}) walked more slowly (118 , 115 , 117 cm s^{-1}) than those in the 75 and 125 cm s^{-1} visual speed conditions (135 and 139 cm s^{-1}). These last speeds are somewhat more normal for instructions to walk rapidly (Durgin et al 2007), suggesting that walking was more normal when visual speeds were appropriate to walking. Because Durgin et al (2005b) 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 figure 3a, were analyzed with an ANOVA with speed (5 levels) and order (walk first or stand first) as between-subjects 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^{-1} . It is possible that more immersive speeds promoted greater multisensory/motor integration.

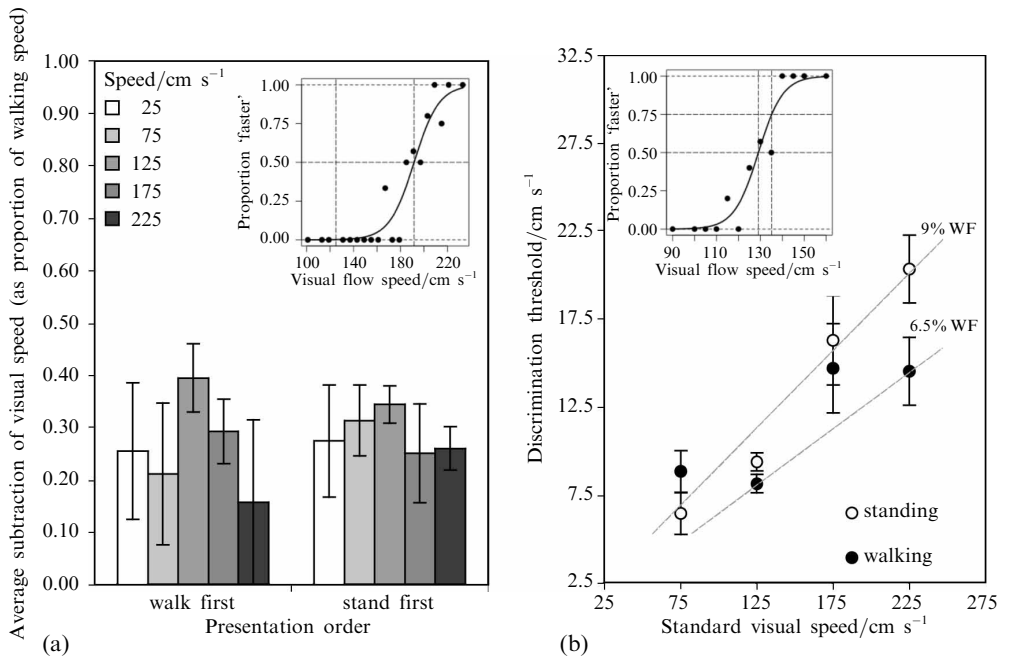


Figure 3. Results of experiments 2 (a) and 3 (b). Values in (a) represent the mean speed subtraction value (\pm SE) expressed as a proportion of walking speed (25–225 cm s^{-1} ; darker bars represent faster standard speeds). Each bar represents the data of five participants. Discrimination thresholds (\pm SE) for optic flow speeds viewed while walking or while standing are shown in (b), where each pair of points represents data from seven or eight participants. For reference, lines representing Weber fractions (WFs) of 9% and of 6.5% are shown. Insets in each graph show sample fits.

3.3 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^{-1}) were tested (with seven or eight participants each). The low speed of the previous experiment (25 cm s^{-1}) 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 min.

3.3.1 *Results and discussion.* Average walking speed did not differ reliably as a function of visual speed in this experiment, and averaged 124 cm s^{-1} overall. Discrimination thresholds are plotted in figure 3b (a sample logistic fit is inset). For three of the four speed conditions these thresholds differed by locomotor state. For those who made judgments of the lowest visual speed (75 cm s^{-1}), performance was better when standing than when walking ($t_7 = 2.03$, $p < 0.05$, one-tailed), whereas for those who judged the highest visual speed (225 cm s^{-1}) and for those who judged the visual speed nearest walking speed (125 cm s^{-1}), discrimination was better while walking than when standing ($t_6 = 3.01$, $p < 0.05$; $t_7 = 2.36$, $p < 0.05$, one-tailed).⁽²⁾ The data for the two speeds that were used in both discrimination experiments (75 cm s^{-1} and 125 cm s^{-1}) closely replicate the discrimination values found in experiment 1, indicating that the earlier results were not artifacts of the speed range used.

4 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 et al 2005b). 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^{-1} (60% of normal walking speed) was impaired by walking in experiment 3 (and had the same trend 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-subjects design in experiment 2, with subtraction of 37% of walking speed for visual speeds near walking speed. On the basis of 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.

Perceptuomotor 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 et al 2003; Durgin et al 2005c). After treadmill locomotion,

⁽²⁾ Although the 'significance' of the result for 125 cm s^{-1} would not survive conservative Bonferroni corrections for multiple tests, this is a replication of a result of experiment 1.

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 et al 1992; Rieser et al 1990; Sun et al 2004b). 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 et al 2005c).

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 et al 2005a). Although biomechanical information may dominate non-visual self-motion perception (Mittelstaedt and Mittelstaedt 2001), it is worth noting that biomechanical activity alone (ie walking on a treadmill) produces less visual speed subtraction than does walking on solid ground (Durgin et al 2005b). 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.

Acknowledgments. This research was supported by Swarthmore College Faculty Research Grant to F Durgin and by a Howard Hughes Medical Institute fellowship to K Gigone. K Gigone is now at the Department of Brain and Cognitive Sciences, University of Rochester. Thanks to Jeff Saunders and Tim Shipley for discussion. Thanks also to three anonymous reviewers for excellent suggestions. Preliminary results of these experiments were presented at the fourth annual meeting of the Vision Sciences Society, Sarasota, FL, May, 2004 and at the 7th Annual International Multisensory Research Forum, Dublin, June 2006.

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ISSN 0301-0066 (print)

ISSN 1468-4233 (electronic)

PERCEPTION

VOLUME 36 2007

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