Exp Brain Res (2004) 154: 246–254
DOI 10.1007/s00221-003-1652-9

RESEARCH ARTICLE

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Multisensory integration in the estimation of relative path length

Received: 23 Janurary 2003 / Accepted: 23 July 2003 / Published online: 6 September 2003

Abstract One of the fundamental requirements for successful navigation through an environment is the continuous monitoring of distance travelled. To do so, humans normally use one or a combination of visual, proprioceptive/efferent, vestibular, and temporal cues. In the real world, information from one sensory modality is normally congruent with information from other modalities; hence, studying the nature of sensory interactions is often difficult. In order to decouple the natural covariation between different sensory cues, we used virtual reality technology to vary the relation between the information generated from visual sources and the information generated from proprioceptive/efferent sources. When we manipulated the stimuli such that the visual information was coupled in various ways to the proprioceptive/efferent information, human subjects predominantly used visual information to estimate the ratio of two traversed path lengths. Although proprioceptive/efferent information was not used directly, the mere availability of proprioceptive information increased the accuracy of relative path length estimation based on visual cues, even though the proprioceptive/efferent information was inconsistent with the visual information. These results convincingly demonstrated that active movement (locomotion) facilitates visual perception of path length travelled.

Keywords Locomotion · Distance perception · Optic flow · Proprioception · Virtual reality

Introduction

One of the fundamental requirements for successful navigation in an environment and the establishment of a mental representation of one's location in space, is the continuous monitoring of distance travelled. Both visual and nonvisual sources of information can potentially be used in this task.

Visual information is often considered to be critical for spatial processing. For instance, the dynamic retinal information generated by the observer's self-motion (optic flow) (Gibson 1950; Lee 1980; Sun et al. 1992; Warren and Hannon 1990), as well as the motion of objects in the environment (Regan and Hamstra 1993; Sun and Frost 1998), can specify the spatial-temporal relation between the observer and environmental landmarks. However, only a few studies have examined the role of optic flow in the estimation of distance travelled (Bremmer and Lappe 1999; Redlick et al. 2001; Witmer and Kline 1998). Results have demonstrated that visual information alone can be used to accurately discriminate and reproduce traversed distances (Bremmer and Lappe 1999).

During navigation, idiothetic information is internally generated as a function of our body movements in space (Chance et al. 1998; Mittelstaedt and Mittelstaedt 2001). This information can be derived from sensory information about movements from muscles and joints ("inflow" or proprioceptive input) and motor efferent signals ("outflow"). The combination of these two kinds of information will be hereafter referred to as proprioception. Another source of idiothetic information is vestibular information, which is generated following a change in linear or rotational movement velocity. Idiothetic information alone can be used to monitor locomotion, as shown by studies demonstrating that humans are able to walk to a previously viewed target without vision (Bigel and Ellard 2000; Elliott 1986; Loomis et al. 1992; Rieser et al. 1990; Steenhuis and Goodale 1988; Thomson 1983). In addition, duration of travel and cognitive factors may also affect the estimation of distance travelled (Foos 1982; Sadalla and Magel 1980; Witmer and Kline 1998).

Compared to studies examining the contributions of particular sensory cues to locomotion, the integration of visual and nonvisual cues has also been explored in a

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variety of tasks such as the estimation of path length (Harris et al. 2000; Ohmi 1996), the reproduction of angular displacement (Lambrey et al. 2002); path integration (Kearns et al. 2002; Klatzky et al. 1998), wayfinding (Grant and Magee 1998), and maintaining a constant walking speed on a treadmill (Prokop et al. 1997).

When multiple sources of information are available in a real-world scenario, they often provide redundant and concordant information, making it very difficult to study the individual contributions of each. Creating cue conflict in multisensory and intrasensory tasks has been a popular approach in identifying the individual contributions of different sensory cues. An influential method has involved the wearing of "displacement prisms," which causes a spatial discrepancy between the shifted spatial layout obtained through vision and the correct spatial layout provided by other sensory modalities such as proprioception (e.g., Pick et al. 1969; Warren 1979). This prism paradigm has typically been used to study the perception of spatial direction as measured through target-pointing responses. A similar method can be adapted to study how travelled distance is perceived during locomotion, which involves dynamic visual and nonvisual information as well as the integration of information over time.

In order to study visual and nonvisual interactions during locomotion, Rieser et al. (1995) adopted an innovative approach to uncouple the natural covariance of vision and proprioception. Subjects were asked to walk on a treadmill at one speed (biomechanical feedback) while being pulled on a tractor at either a faster or a slower speed (environmental flow feedback). Subjects' path length estimations were altered after having experienced a new relation between locomotor activity and the resulting optic flow. However, these results may not be generalizable due to the fact that the sensory stimulation may not have been well controlled (e.g., the presence of extraneous visual and nonvisual stimulation) and subjects may have been aware of the experimental manipulation.

In the current study we adopted an efficient, reliable, and systematic approach by simulating locomotor experiences in a virtual environment. Subjects' task involved moving forward down a straight, virtual hallway. The perceptual experience of moving in the virtual environment was created when subjects pedalled a stationary bicycle while simultaneously being presented with the corresponding optic flow information. The optic flow information was yoked directly to subjects' pedalling movements. The relation between visual and proprioceptive information was varied through software by manipulating optic flow gain (OFG: the relation between subjects' pedalling speed and the resulting speed of the visual flow field). In this task, proprioceptive information was available while vestibular information was mainly excluded.

Our paradigm was different from commonly utilized cue-conflict paradigms in terms of how the "conflict" was created. In a prism paradigm, when a horizontal wedge prism is used, there is an absolute discrepancy at any given moment in egocentric directional information received from vision (displaced direction) and from proprioception (correct direction). However, for locomotion tasks, without a scaling factor, there is no absolute coupling between optic flow and proprioceptive information at any single moment. Optic flow, however, can provide relative velocity or distance information (Bremmer and Lappe 1999). We thus used a psychophysical ratio estimation task comparing two travelled path lengths to examine how subjects were able to estimate path length travelled. Our virtual reality (VR) paradigm allowed us to change the relation between visual information and proprioceptive information across different travelled path lengths. This approach permitted the first assessment of the individual contributions of optic flow information and of proprioceptive information in relative path length estimation.

Materials and methods

Subjects

Thirty-three subjects (17 females and 16 males) participated in this study with ages ranging from 19 to 24, all with normal or corrected-to-normal visual acuity. All subjects gave their informed consent prior to their inclusion in this study. This research was approved by the McMaster University Research Ethics Board and has therefore been performed in accordance with the ethical standards specified by the 1964 Declaration of Helsinki.

Stimuli

The VR interface was a modified stationary mountain bicycle (see Fig. 1A). The rear tire of the bicycle was equipped with an infrared sensor that translated pedalling speed information to an SGI Onyx2 with an Infinite Reality2 Engine. The visual environment was developed using Open Inventor and was presented to subjects via a head-mounted display (V8, Virtual Research; liquid crystal display with a resolution of 640×480 per eye and a field of view of 60° diagonal), which presented the same image to both eyes. The environment consisted of a straight, empty, seemingly infinite hallway with walls, a floor, and no ceiling. Both the floor and the two walls were covered with a completely random dot texture (see Fig. 1B).

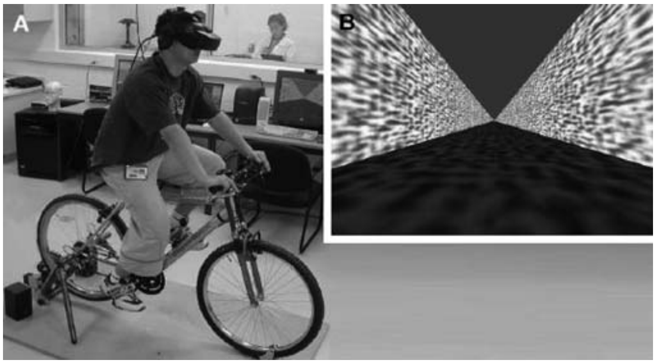

Fig. 1. A Subjects wore a head-mounted display and rode a stationary bicycle in order to move through the virtual world. **B** The visual environment consisted of a straight, empty, and seemingly infinite hallway

Procedure

Prior to the experiment, each subject was given explicit instructions on the task and was provided with a series of practice trials (without feedback) to get used to both the equipment and the task.

Subjects pedalled the stationary bicycle at a comfortable speed and attempted to maintain that pedalling speed throughout each trial. As a direct effect of their own pedalling movements, subjects simultaneously experienced the visual flow pattern via the head-mounted display in real time. The information about subjects' pedalling movement was used both to update the visual information and for the purpose of subsequently analyzing subjects' movement dynamics (e.g., pedalling speed).

Each trial required subjects to travel through two path lengths: an initial "reference" path length followed immediately by a "judgement" path length. The end of each path was indicated by a loud clicking sound, at which point subjects were required to stop pedalling. At the end of the trial, subjects were asked to give a verbal estimation of the judgement path length as a percentage of the reference path length. Subjects were instructed to provide estimates that were as precise as possible and subjects' actual estimations tended to fall in 5% increments. No feedback of any kind was given. The reference path lengthwas always kept fixed at a length equivalent to the real-world length of 32 m, while the judgement path length was varied randomly among a number of lengths.

As stated previously, OFG is defined as the relation between the information received visually and the information received through nonvisual (proprioceptive) sources. Considering subjects pedalling speed was on average one pedal rotation per second, when an OFG of 1 was specified by the VR software, subjects visually perceived a speed of 4 m/s. Thus, if subjects produced eight pedal rotations (over 8 s), they would visually experience a reference path length of 32 m. For the same pedalling speed, when presented with an OFG of 2, subjects would visually perceive a speed of 8 m/s. Thus, subjects would only need to produce four pedal rotations (over 4 s) in order to visually experience the path length of 32 m. We can think of the OFG manipulation as being somewhat analogous to switching the gears on a bicycle without having the normal accompanying change in required muscle strength or exertion.

The experiment consisted of four conditions administered in a random order. In condition 1, relative path length estimation was tested using a simulated normal bicycle riding experience. In this condition, the OFG was held constant at 1 throughout the test. As a result, the relation between the information received visually and the information received through nonvisual sources was consistent throughout the condition. This condition will hereafter be referred to as the VN_{con} condition. In this condition, the reference path length was held at a visually specified length of 32 m. The judgement path length was varied randomly among 21 lengths ranging from 18% to 200% of the reference path length. Each subject was tested with four blocks of 42 trials.

In condition 2 the OFG was varied randomly. Such variations produced an inconsistent relation between the visual and nonvisual information between trials as well as between the reference and judgement path lengths presented during each trial. This condition will hereafter be referred to as the VN_{incon} condition. In this condition, one of four values of OFG (0.31, 0.77, 1.23, and 1.69) was assigned randomly to both the reference path length and the judgement path length. The reference path length was held constant at a visually specified length of 32 m, but because the OFG was varied among four levels, the path length specified by proprioceptive information varied among four values. The judgement path length specified by vision was varied randomly among nine levels. In order to include all four optic flow gains for each of the nine visually specified lengths, the length specified by proprioceptive information would have to vary among 36 levels. Each subject was tested with four blocks of 36 trials.

In condition 3, subjects viewed the same pattern of optic flow as in the VN_{incon} condition through the head-mounted display; however, their movement was generated by operating a computer mouse rather than riding the bicycle. Due to the fact that subjects did not pedal the bicycle, the proprioceptive information provided by leg movements was removed. This condition will hereafter be referred to as the $P_{(-)}$ condition. Each subject was tested with four blocks of 36 trials.

In condition 4, visual information was absent and will hereafter be referred to as the $V_{(-)}$ condition. All aspects of this condition were the same as those in the VN_{con} condition, with the exception that subjects pedalled in the dark. Each subject was tested with four blocks of 42 trials.

For the VN_{con}, VN_{incon}, and $V_{(-)}$ conditions, if subjects pedalled at a constant speed, the information from proprioceptive sources and duration of travel were always matched; thus, it would not be possible to distinguish the contributions of each source. In the $P_{(-)}$ condition, although proprioceptive information was removed, duration of travel remained a possible source of nonvisual information.

Results

Figures 2, 3, 5, 6 and 7 illustrate the relation between subjects' relative path length estimates (L_{est}) and the correct path length (L) for the various conditions. If subjects estimated path length perfectly, it would be expected that their responses would fall on the diagonal dashed line. The difference between the mean estimated response and the correct response is considered constant error.

Errors for the VN_{con} condition

Figure 2 illustrates the relation between the mean L_{est} and L when OFG was consistent (VN_{con} condition). When the judgement path length was longer than the reference path length (correct response higher than 100%), subjects tended to underestimate the length. As the path length increased, the constant error increased somewhat proportionally. Errors were minimal when the judgement path lengths were shorter than the reference path lengths. The standard deviation of the path length estimate tended to increase slightly as the judgement path length increased.

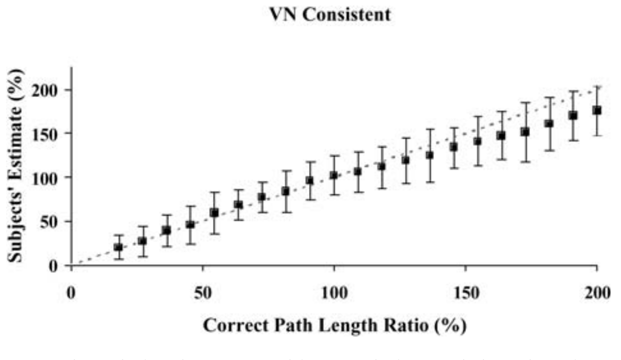

Fig. 2 The relation between subjects' relative path length estimates (L_{est}) and the correct path length (L) in the VN_{con} condition. The *diagonal dashed line* indicates perfect performance. The *error bars* represent standard deviation

Errors for the VN_{incon} and $P_{(-)}$ conditions

Errors should subjects exclusively use visual information

In the VN_{con} condition, the path length information obtained from visual inputs, nonvisual inputs, or both, would lead to the same estimate. Thus, the contributions of different sensory cues were not distinguishable in this case. However, for the VN_{incon} condition, if subjects were to rely exclusively on information from visual inputs or from nonvisual inputs (proprioception and/or duration of travel), this would lead to different responses. The correct path length, if subjects' responses were based exclusively on visual cues (L_v) or exclusively on nonvisual cues (L_n), was calculated independently. L_v was calculated using the ratio of judgement path length to reference path length.

During the VN_{incon} condition, the relation between the mean L_{est} and the mean L_v is illustrated in Fig. 3A. The constant errors in relative path length estimation were larger in magnitude when the judgement path length was either much longer or much shorter than the reference path length (further away from 100%). When the judgement path length was longer than the reference path length, subjects tended to underestimate the length, whereas when the judgement path length was shorter than the reference path length, they overestimated. The size of the constant errors appeared to be larger in the VN_{incon} condition (Fig. 3A) than in the VN_{con} condition (Fig. 2).

In the $P_{(-)}$ condition (Fig. 3B) magnitude of error was larger than in the VN_{incon} condition (Fig. 3A), although the pattern of error was similar, i.e., there was an underestimation for the longer path lengths and an overestimation for the shorter path lengths. To compare the size of error between the VN_{incon} condition and the $P_{(-)}$ condition, a statistical test comparing the slope of the regression lines for these two conditions demonstrated that the magnitude of error for the $P_{(-)}$ condition was significantly greater (t-test, $p<0.05$, Zar 1996, pp 353–357).

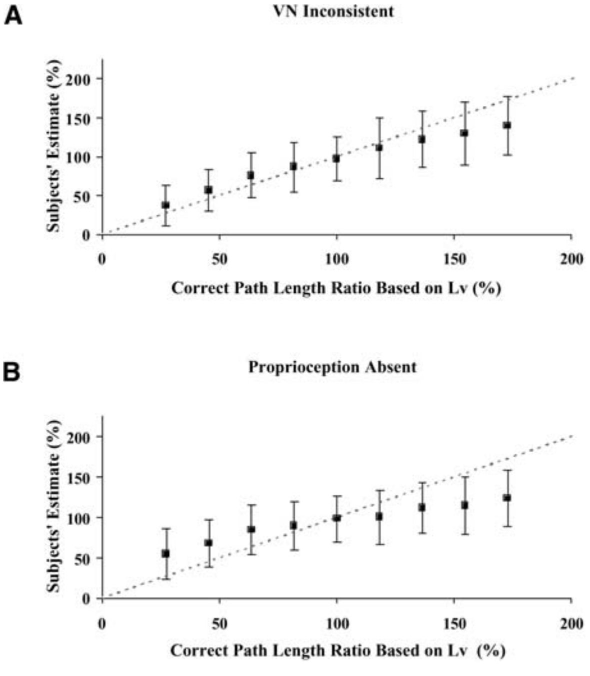

Fig. 3A, B The relation between subjects' relative path length estimates (L_{est}) and the correct path length as specified by vision (L_v) for the VN_{incon} condition (**A**) and for the $P_{(-)}$ condition (**B**)

As a result of the higher magnitude of error observed in the $P_{(-)}$ condition, estimates appeared to be similar across path lengths (Fig. 3B). In order to test whether subjects were performing at chance levels, we conducted an ANOVA which demonstrated that the variations among the path length estimates were in fact significantly different ($F_{(8,296)}=114$, $p<0.001$).

For a given path length, the variation of subjects' relative path length estimations is considered variable error. Overall, the standard deviation of the path length estimate tended to increase slightly as the judgement path length increased. This is evident in the VN_{incon} condition (Fig. 3A), but less so in the $P_{(-)}$ condition (Fig. 3B).

Errors should subjects exclusively use visual information: effect of OFG

For both the VN_{incon} condition and the $P_{(-)}$ condition, the above analysis was conducted on data that was collapsed across all levels of OFG. To assess whether the error fluctuated as a function of OFG, Fig. 4A, B illustrates subjects' estimates broken down into the four levels of OFG (in judgement path length) for the VN_{incon} and $P_{(-)}$ conditions, respectively. It appears that the magnitude of error differed as a function of OFG, with larger OFGs resulting in larger constant error. A 4×9 (4 OFGs × 9 path lengths) within-subjects ANOVA was conducted for each condition. For the VN_{incon} condition, there was no significant effect of OFG ($F_{(3,96)}=1.77$, $p>0.05$); however, there was a significant effect of path length ($F_{(8,256)}=59.44$, $p<0.001$). Further, a significant interaction effect between OFG and path length was observed ($F_{(24,768)}=2.18$, $p<0.001$). For the $P_{(-)}$ condition, there was a significant effect of OFG ($F_{(3,96)}=6.58$, $p<0.001$) and a significant effect of path length ($F_{(8,256)}=156.39$, $p<0.001$). Further, a significant interaction effect between OFG and path length was observed ($F_{(24,768)}=2.54$, $p<0.001$). The results suggest that the effect of optic flow is non-linear and such non-linearity is not uniform for different path length ratios.

Errors should subjects exclusively use nonvisual information

The correct path length, if subjects' responses were based exclusively on nonvisual cues (L_n), was calculated using the ratio of travel duration of the judgement path length to the travel duration of the reference path length. The duration of travel was calculated by assuming that subjects always pedalled at a constant speed.

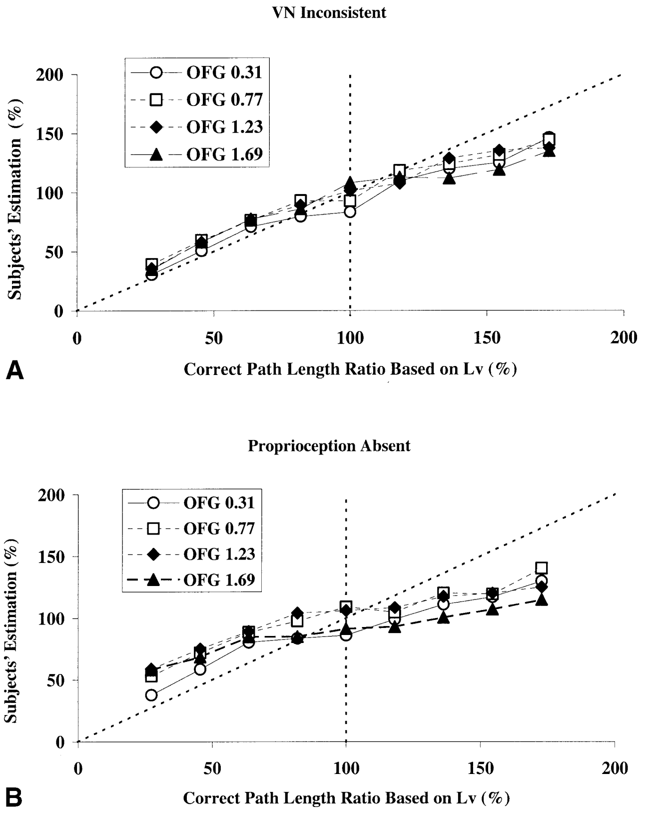

Fig. 4A, B The relation between subjects' relative path length estimates and the correct path length as specified by vision (L_v) plotted according to different levels optic flow gain (OFG) used in judgement path, for the VN_{incon} condition (**A**) and for the $P_{(-)}$ condition (**B**)

Figure 5A, B illustrates the relation between the mean L_{est} and the L_n for the VN_{incon} and $P_{(-)}$ conditions, respectively. Figure 6A, B further clarifies this relation by focusing on the range between 25% and 175% of the correct answers in Fig. 5A, B. Both constant error and variable error were high. This suggests that when visual information was inconsistent with nonvisual information, relative path length estimation was not directly derived from nonvisual sources.

Error for the $V_{(-)}$ condition

When visual information was absent ($V_{(-)}$) (Fig. 7), the pattern of error and the magnitude of error were comparable to the VN_{con} condition (Fig. 2). This indicated that nonvisual information alone was sufficient for relative path length estimation. The variable error increased proportionally as the judgement path length increased. The magnitude of the variable error in the $V_{(-)}$ condition was somewhat larger than that in the VN_{con} condition.

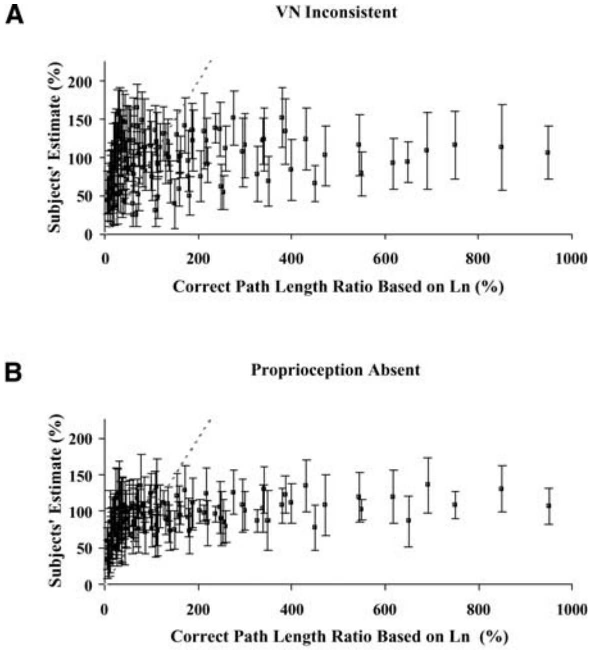

Fig. 5A, B The relation between subjects' relative path length estimate (L_{est}) and the correct path length as specified by nonvisual information (L_n) across the entire range of path lengths tested, for the VN_{incon} condition (**A**) for the $P_{(-)}$ condition (**B**)

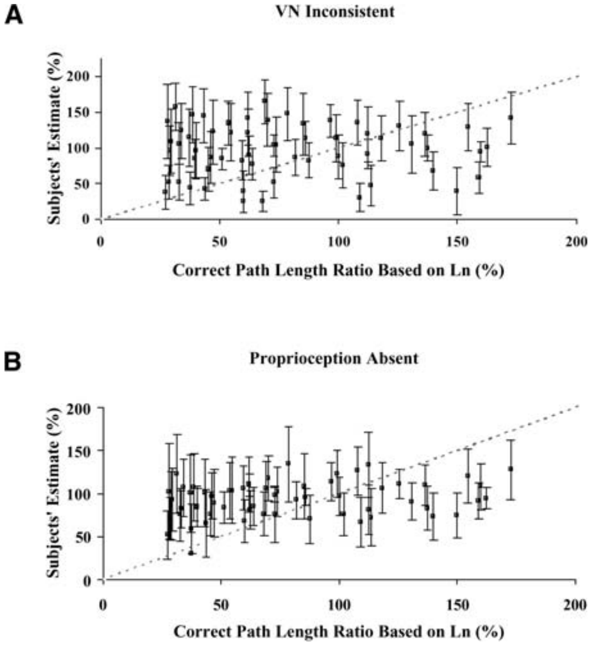

Fig. 6A, B The relation between subjects' relative path length estimate (L_{est}) and the correct path length as specified by nonvisual information (L_n) for the range of path lengths between 25 and 175% of the correct answers, for the VN_{incon} condition (**A**) and for the $P_{(-)}$ condition (**B**)

Summary of errors

Figure 8 illustrates the mean unsigned errors (combination of constant and variable errors) for all path lengths and for all subjects tested in each condition. There was no

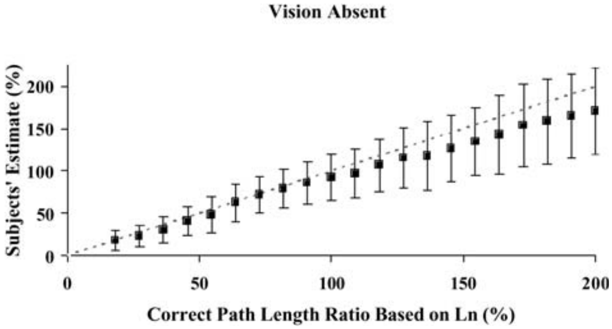

Fig. 7 The relation between subjects' relative path length estimate (L_{est}) and the correct path length as specified by nonvisual information (L_n), for the $V_{(-)}$ condition

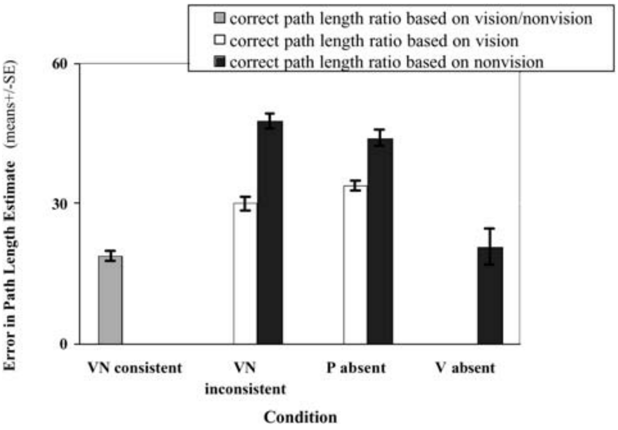

Fig. 8 The mean unsigned errors across all path lengths for all conditions. *V* visual information, *N* nonvisual information, *P* proprioceptive information, *VN* combination of visual and nonvisual information

significant difference between the VN_{con} and the $V_{(-)}$ conditions (t(32)=0.5, $p>0.05$), indicating comparable performance for the conditions in which visual and nonvisual cues were consistent and when nonvisual cues were presented alone.

In addition, the magnitude of error for the VN_{con} condition was smaller than the magnitude of error observed for both the VN_{incon} and $P_{(-)}$ conditions assuming subjects relied exclusively on visual information (t(32) =2.78, $p<0.001$).

For both the VN_{incon} and the $P_{(-)}$ conditions, the magnitude of error for L_v was much less than for L_n, indicating vision's dominance (VN_{incon}, t(32)=10.26, $p<0.001$; $P_{(-)}$, t(32)=5.0, $p<0.001$) (see Fig. 8). This comparison was made by averaging only the data for L_n within the range equivalent to that of L_v (i.e., when the correct answer was between 25 and 175%, see Fig. 6A, B). Note that such a comparison represents a more conservative estimate of the overall difference in error observed between the two cues. If the entire range of path lengths as specified by nonvisual information (5–950%) were considered, the error should subjects rely exclusively on nonvisual cues would be much higher, with a mean error of 99.6 for the VN_{incon} condition and 98.1 for the $P_{(-)}$ condition.

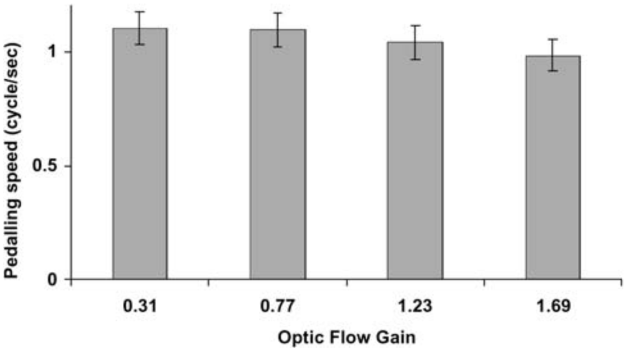

Fig. 9 The relation between subjects' average pedalling speed and OFG for the VN_{incon} condition

Assuming that subjects used exclusively visual information, the error was significantly smaller for the VN_{incon} condition than for the $P_{(-)}$ condition (t(32)=2.78, $p<0.01$), indicating that the presence of proprioceptive cues improved performance even though they were inconsistent in relation to the visual cues. For L_n, there was no significant difference between the VN_{incon} and the $P_{(-)}$ conditions (t(32)=1.3, $p>0.05$).

Effect of OFG on pedalling speed

It is important to note that for the VN_{incon} condition, the calculation of correct path length specified by nonvisual information was made on the basis that subjects pedalled the bicycle at a constant speed. We also empirically examined whether subjects' actual pedalling speed fluctuated in response to the different OFGs presented. To do this, each subject's average pedalling speed for each trial was calculated by measuring the last 2 s of pedalling movement. Speed values were then averaged for each subject across all trials for each OFG used. As shown in Fig. 9, subjects tended to pedal slightly slower for higher OFGs. Such differences in pedalling speed were significant as indicated by a one-way ANOVA comparing the four levels of OFG ($F_{(3,96)}=27.4$, $p<0.001$). However, these differences in pedalling speed (ranging from 1.1 to 0.9) were minimal compared to the corresponding differences in OFG (ranging from 0.31 to 1.69).

Discussion

The present study investigated the relative contributions of optic flow information and proprioceptive information to human performance on relative path length estimation. During the VN_{con} and $V_{(-)}$ conditions, subjects produced the least amount of error, suggesting proficiency in relative path length estimation using either combined cues or nonvisual cues alone. In the VN_{incon} condition, estimations appeared to be based predominantly on L_v. Thus, when visual and proprioceptive information were inconsistent with each other, subjects responded in a manner as predicted should optic flow remain the dominant source of information. What is of particular interest is that, although proprioceptive information was not used directly, its mere availability increased the accuracy of relative path length estimation based on visual cues, even though the proprioceptive information was inconsistent with the visual information.

Visual dominance and the unique role of proprioceptive information

The visual dominance reflected in the path length estimates for the VN_{incon} condition is similar to what has been observed in cue-conflict literature examining visual-tactile interactions in near body space (Warren and Rossano 1991; Welch 1978; Welch and Warren 1986). For example, it has been shown that when subjects are required to wear displacement prisms, causing a spatial discrepancy between the shifted spatial layout obtained through vision and the correct spatial layout provided by nonvisual cues, they predominantly rely on vision to perform spatial tasks (e.g., Pick et al. 1969; Warren 1979).

In our VN_{incon} condition, proprioceptive information actually provided "conflicting" information with regards to visual information. It would be reasonable to assume that should the conflicting proprioceptive information be removed, as was the case in the $P_{(-)}$ condition, the accuracy of relative path length estimation based on visual information should increase. This was in fact the opposite of what we found. The fact that subjects' performance based on vision dropped with the removal of proprioceptive cues demonstrated for the first time that the proprioceptive information involved in active movement improves the encoding of the resulting optic flow information, even when the proprioceptive information is misleading.

It seems reasonable to claim that combining proprioceptive information with visual input would be advantageous. When subjects are actively engaging in a locomotor activity, it is possible that they may have a stronger tendency to register the resulting visual flow information, making the relative path length estimation based on vision more likely and more accurate. Indeed, literature has demonstrated that idiothetic updating facilitates visual performance regarding both stationary landmarks (e.g., object recognition, Harman et al. 1999) and the spatial relation between objects (Simons and Wang 1998). This improved perception due to action is an interesting cross-modal interaction that complements theoretical frameworks that discriminate vision-for-perception from vision-for-action (Milner and Goodale 1996).

Cue interaction models

To some extent, our results are in accordance with the general ideas specified by the statistically optimal integration model that has recently received convincing support from work on visual-haptic integration (Ernst and Banks 2002; van Beers et al. 1999, 2002) and on the integration of different visual cues in depth perception (Johnston et al. 1993; Johnston et al. 1994; Young et al. 1993). This theory predicts that sensory information from multiple sources is weighted according to the estimated reliability of each source relative to the estimated reliabilities of other available sources. A number of aspects of our study are consistent with this model.

In our study, when the relation between visual and nonvisual information was variable, the results showed that subjects tended to rely more heavily on visual information. Such results may reflect the perceived reliability of these two cues in the current path length estimation task. It has traditionally been demonstrated that visual cues are, in general, more informative for large scale spatial processing than any other sensory information (Warren and Rossano 1991).

With regards to nonvisual information, duration of travel may potentially contribute to path length estimation. Therefore, in the VN_{incon} condition, visual information, proprioceptive information, and duration of travel may all be contributing cues. In the $P_{(-)}$ condition, only visual information and duration of travel were available. If the combined visual-proprioceptive information available in the VN_{incon} condition was perceived as being more reliable, this combination would be more heavily weighted during path length estimation compared to situations in which proprioceptive cues were absent ($P_{(-)}$). Consequently, the apparent advantage of using a combination of cues appeared to persist even when the two sources of information were not consistent across trials.

In contrast to our results, Kearns et al. (2002) assessed path integration using a VR walking paradigm. It was demonstrated that when nonvisual information generated from walking was combined with intermittently available optic flow information, subjects relied more heavily on nonvisual cues. Although their results seemed to contradict our results, this discrepancy may in fact be a direct consequence of the differences in experimental design. For instance, in the Kearns et al. experiment, optic flow information was only intermittently available and therefore may have been perceived as being less reliable than nonvisual information. Further, because in their study locomotion was achieved through walking, this may have offered a more reliable source of nonvisual information than pedalling a stationary bicycle, a task not as common as walking.

Although our results regarding visual-proprioceptive interaction appear to be consistent with the general assumptions specified by the statistically optimal integration model in terms of cue weighting based on perceived reliability, the exact nature of the cue combination requires further examination. Experiments supporting the optimal integration model typically use very subtle sensory conflicts (e.g., Ernst and Banks 2002) and these results suggest that subjects' estimations were based on a weighted average of individual cues (Clark and Yuille 1990). Our experiment involved a greater sensory "conflict" between vision and proprioceptive information.

Our results indicated that, although nonvisual information was not used directly, the mere availability of proprioceptive information increased the accuracy of relative path length estimation based on visual cues, even though the proprioceptive information was inconsistent with the visual information. Therefore, it appears that the interaction between visual and proprioceptive information found in our study takes a different and non-linear form compared to the results reported in other literature which demonstrates a linear weighting (e.g., Johnston et al. 1994; Young et al. 1993).

Similar to the cue interaction mechanisms discussed in the context of visual-haptic interactions, Mittelstaedt and Mittelstaedt (2001) described three forms of interactions that may occur between vestibular and proprioceptive cues when estimating path length. Vestibular cues could either be suppressed by the proprioceptive cues, cancelled by the proprioceptive cue (see also Mergner and Rosemeier 1998), or the two cues could actually combine to form an optimized weighted average. The results of the current study examining relative path length estimation revealed a unique interaction between visual and proprioceptive cues that may not be entirely explained by other proposed theories. In order to gain a better understanding of such mechanisms, further experimentation involving the quantification of path length discrimination thresholds would complement the current findings involving ratio estimation.

The effect of optic flow on pedalling speed

In our study, in addition to being required to monitor and report the path length travelled, subjects were also responsible for maintaining a constant pedalling speed. Both of these tasks required subjects to monitor visual and nonvisual information.

Results showed that pedalling speed varied slightly as a function of OFG, but not to the degree that would be predicted should pedalling speed be completely determined by OFG (Fig. 9). As shown in the VN_{incon} condition, the strong contribution of visual information in the estimation of path length appears to be inconsistent with the results of the small effect of OFG on the rate of pedalling. The fact that subjects relied more heavily on different sources of sensory information when estimating path length compared to when maintaining a constant pedalling speed may reflect differences in task requirement. When subjects were required to monitor and report path length, visual information seemed to play a more important role, perhaps reflective of the fact that vision is normally the more reliable and more readily available source of information for spatial perception. In contrast, when subjects were required to maintain a constant pedalling speed, they may have devoted more attention to proprioceptive information, as it typically provides more reliable locomotor information.

The magnitude of the effect of optic flow on pedalling speed is consistent with the effect of optic flow found in studies using a treadmill-walking task. Prokop et al. (1997) conducted a study in which subjects were instructed to walk at a constant speed on a closed-loop treadmill while the magnitude of optic flow was manipulated. Their results demonstrated that subjects modulated their movements as a result of variations in optic flow magnitude. However, the degree to which subjects modified their movements was far less than predicted should subjects only rely on optic flow. Overall, both Prokop et al. and the current study suggest that both visual and proprioceptive information play a role in modulating self-motion—findings that are generally consistent with other similar studies (Konczak 1994; Stappers 1996; Varraine et al. 2002).

As shown in the VN_{incon} condition, not only did pedalling speed vary slightly as a function of OFG (Fig. 9), but the verbal estimates of relative path length also differed according to OFG (Fig. 4). In other words, the effect of visual speed was non-linear. Mittelstaedt and Mittelstaedt (2001) also showed that path length estimation varied in response to changes in movement speed when idiothetic cue availability was manipulated. In our study, although subjects' pedalling speed remained within a small range, the variation in OFG and thus the variation in visual speed led to a non-linearity similar to that observed with regards to idiothetic cues (Mittelstaedt and Mittelstaedt 2001). The exact pattern and nature of such visual non-linearity remains to be examined extensively and could be better understood with additional experimental conditions designed to isolate the contributions of optic flow.

Conclusion

This is the first study to investigate the relative contributions of visual and proprioceptive information in relative path length estimation. Further, it complements literature investigating the relative contributions of these sources of information to locomotion in general. The results of this study will allow for further examination of the exact nature of such interactions. For instance, it is important to evaluate whether the beneficial effect of proprioceptive information is strictly a perceptual phenomenon or results from the fact that subjects have active control over their movement and/or experience increased levels of attention. Ultimately, this paradigm allows for further insight into how the brain integrates different sources of information.

Acknowledgements The authors wish to thank Drs. D. Maurer, R. Racine, L. Allan, and C. Ellard for helpful discussions and comments on the manuscript and N. Jones, K. Strode, and D. Zelek for their assistance in collecting data. We would also like to thank Dr. B. Frost, G. Barrett, and R. Dupras for discussions and assistance in the initial design and construction of the VR interface and software. We also thank two anonymous reviewers for helpful comments on the earlier versions of this article. This work was supported by grants from the Natural Science and Engineering Research Council of Canada and the Canadian Foundation for Innovation to H.-J.S.

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