

# Multisensory Integration in Speed Estimation During Self-Motion

HONG-JIN SUN, Ph.D., AMANDA J. LEE, B.Arts.Sc.(H), JENNIFER L. CAMPOS, B.A.(H),  
GEORGE S.W. CHAN, B.Sc.(H), and DA-HUI ZHANG, B.Eng.

## ABSTRACT

This study assessed the relative contributions of visual and proprioceptive/motor information during self-motion in a virtual environment using a speed discrimination task. Subjects wore a head-mounted display and rode a stationary bicycle along a straight path in an empty, seemingly infinite hallway with random surface texture. For each trial, subjects were required to pedal the bicycle along two paths at two different speeds (a standard speed and a comparison speed) and subsequently report whether the second speed travelled was faster than the first. The standard speed remained the same while the comparison speed was varied between trials according to the method of constant stimuli. When visual and proprioceptive/motor cues were provided separately or in combination, the speed discrimination thresholds were comparable, suggesting that either cue alone is sufficient. When the relation between visual and proprioceptive information was made inconsistent by varying optic flow gain, the resulting psychometric functions shifted along the horizontal axis (pedalling speed). The degree of separation between these functions indicated that both optic flow and proprioceptive cues contributed to speed estimation, with proprioceptive cues being dominant. These results suggest an important role for proprioceptive information in speed estimation during self-motion.

## INTRODUCTION

RECENT DEVELOPMENTS IN VIRTUAL REALITY (VR) technology have opened many doors for studying human performance for a number of reasons. A virtual environment provides a much more ecologically valid and realistic experience for subjects compared to those provided by traditional perceptual and cognitive experiments. For instance, the sense of “presence”—the subjective experience of being within an environment, is much greater in a virtual environment than a simple desktop display. Further, VR paradigms can provide richer sensory feedback to subjects than typical experiments conducted with a standard computer display and input device.<sup>1</sup> In the past few years, through advanced technology,

researchers have been able to develop VR interfaces that allow natural body movements to be yoked to a visual display, thus, gaining important insights into human spatial processing.<sup>2,3</sup> In addition, VR allows experimenters to create artificial experimental scenarios that could not be implemented in the real world.

In the past few years, one area of study that has benefited from VR technology is the study of multisensory integration. When one navigates in a natural environment, multiple sources of sensory information are available. For instance, visual information can be derived from a variety of sources such as, static environmental cues, object motion cues,<sup>4,5</sup> as well as “optic flow” cues—the apparent movement of the entire visual field in the opposite direction of the ob-

server's movement.<sup>6-9</sup> In addition, multiple sources of nonvisual information are also available during self-motion. For instance, idiothetic information is internally generated as a function of our body movement in space.<sup>2,10</sup> One source of idiothetic information is provided by proprioceptive cues that are derived from both muscles and joints (inflow) and from motor efferent signals (outflow). Another source of idiothetic information is provided by vestibular cues that are derived from changes in linear and/or rotational movement speed.

Information that is particularly important for monitoring self-motion is movement speed. Studies have examined how different components of optic flow influence speed estimation.<sup>11</sup> This has been further investigated through the examination of speed discrimination thresholds<sup>12</sup> and through examining subject's ability to detect changes in speed.<sup>13</sup> It is important to note that, in these studies sensory information was limited to visual cues.

While much has been discovered about the contributions of vision in speed perception, less is understood about the relative contributions of visual and nonvisual information when both are available. Although vision and proprioception are suspected to play a central role in assessing speed information, it is not clear which modality is more important for monitoring speed of self-motion.<sup>14-19</sup> While visual information is often considered to be dominant as compared to other sensory information in most spatial tasks, studies examining human self-motion has called this assumption into question. Data from previous studies suggested that when humans were instructed to maintain a constant walking speed, they weighed the information gained from proprioceptive cues higher than visual cues.<sup>15-19</sup>

When multiple sources of information are available in a real world scenario, they often provide concordant information making it very difficult to study the individual contributions of each. Creating cue conflict in multisensory tasks has been a popular approach in identifying the individual contributions of different sensory cues in spatial processing. One influential method involves the wearing of "displacement prisms," which causes a spatial discrepancy between the shifted spatial layout obtained through vision and the correct spatial layout obtained through other sensory modalities such as proprioception.<sup>20,21</sup> This prism paradigm has typically been used to study the perception of spatial direction through measuring target-pointing responses. A similar method can be adopted to study sensory integration during locomotion.

In order to study visual and nonvisual interactions during locomotion, Rieser et al.<sup>22</sup> adopted an

innovative approach to uncouple the natural covariance of these two cues. Subjects were asked to walk on a treadmill that was being pulled by a tractor. This resulted in subjects experienced a visual speed that differed from their proprioceptive speed. Subjects' responding was reflective of the degree of discrepancy between locomotor activity and the resulting optic flow. However, these results may not be generalizable due to the fact that subjects may have been aware of the experimental manipulation and the sensory stimulation may not have been well controlled (e.g., the presence of extraneous visual and nonvisual stimuli).

In the current study, we developed an efficient, reliable, and systematic approach to study a similar question by incorporating locomotor experiences into a VR paradigm. Subjects were required to move forward along a straight, seemingly infinite virtual hallway. The perceptual experience of moving in the virtual environment was created when subjects' pedalled a stationary bicycle and viewed the resulting optic flow information through a head-mounted display (HMD). The relation between visual and proprioceptive cues was varied through software by manipulating the optic flow gain (OFG) as defined as the relation between subjects' pedalling speed and the resulting speed of the visual flow field. In this task, proprioceptive cues were available while vestibular cues were mainly excluded.

Our paradigm differed from commonly employed 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 between the 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, provides *relative* speed information for movement.<sup>23</sup> Using a VR paradigm, we tested subjects' ability to discriminate between two speeds experienced within the same virtual environment. Subjects' responses were used to determine the just noticeable difference (JND) for each presented speed. Conflicting visual and proprioceptive cues were expected to bring about a directional shift in the psychometric functions. In addition to evaluating the contributions of visual and proprioceptive cues during sensory conflict, the availability of each cue was also independently manipulated. This approach permitted the first assessment of the relative contributions of optic flow information and proprioceptive information in speed discrimination.

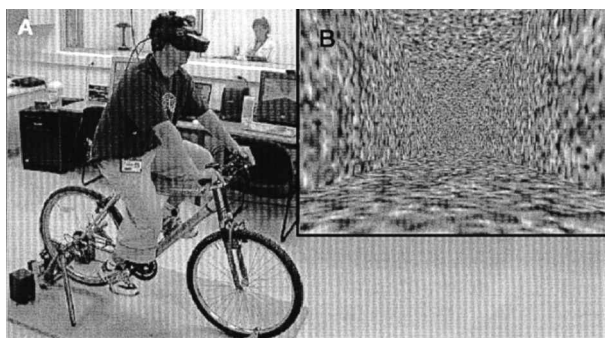
## MATERIALS AND METHODS

### Subjects

Fifty subjects (22 males and 28 females) participated in this study with ages ranging from 19 to 24, all with normal or corrected-to-normal visual acuity. Among the overall 50 subjects, 9 subjects were included in Condition 1, 20 were included in Condition 2, 12 were included in Condition 3, and 9 were included in Condition 4. A detailed description of each condition will be described below. Subjects were undergraduate students from McMaster University who participated in the experiment for course credit or money. All subjects gave their informed consent prior to their inclusion in this study. This research was approved by the McMaster University Research Ethics Board.

### Apparatus

The VR interface used in this experiment included a modified stationary mountain bicycle (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 information generated from the pedalling movements updated the visual environment. The visual environment was developed using Open Inventor and was presented to subjects via a HMD (V8, Virtual Research, liquid crystal display with a resolution of  $640 \times 480$  per eye and a field of view of  $60^\circ$  diagonal), which presented the same image to both eyes. The HMD was equipped with earphones that allowed for the presentation of auditory signals. An additional pair of soundproof ear muffs were worn on top of the earphones on the HMD to block out all outside noise. The visual en-



**FIG. 1.** (A) Subjects wore a HMD 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.

vironment consisted of a straight, empty, seemingly infinite hallway, with walls, a floor, and a ceiling. All surfaces were covered with a random dot texture (Fig. 1B).

### Procedure

Prior to the experiment, each subject received explicit instructions on the task and were given a series of practice trials to become familiar with both the equipment and the task. As a direct consequence of subjects' own pedalling movements, the visual flow pattern was simultaneously updated (yoked to the pedalling movement) in real time and viewed via the HMD. Each trial required subjects to travel through the same hallway twice at two different speeds: an initial standard speed followed immediately by a comparison speed. Upon completion of the trial, subjects were asked to judge whether the second speed was faster than the first speed. No feedback of any kind was given. The standard pedalling speed was always kept fixed at 100 virtual units, which can be considered equivalent to the real world pedalling speed of 1 pedal rotation per second, or 15 km per hour for the bicycle gear used. The comparison speed was varied randomly among nine values (from 60 to 140 virtual units) based on the method of constant stimuli. The comparison speeds were presented in a random order.

To achieve the predefined speed values, subjects were instructed to pedal at varying speeds until they heard a tone indicating that they had reached a desired speed range (within an interval of  $\pm 7.5\%$  of the predefined speed value). They were then required to maintain that speed, as indicated by the continuation of the tone for 2 sec, following which they were prompted by a message on the screen to terminate the movement.

Each subject participated in only one of the four experimental conditions as described below. In condition 1, the OFG was held constant and veridical (at a value of 1) throughout the test. As a result, the relation between the information received visually and the information received through proprioceptive sources were consistent throughout the condition. This condition will hereafter be referred to as the  $VP_{con}$  condition.

In condition 2, the visual display remained yoked to the pedalling movement. One of three OFG values (1.17, 1, and 0.83) was randomly assigned to the comparison speed, while an OFG value of 1 was assigned to the standard speed. Manipulating OFG can be considered somewhat analogous to switching the gears on a bike without having the normal accompanying changes in required muscle strength or exer-

tion. For example, if subjects were to pedal down two hallways at the same speed while being presented with two different OFGs (e.g., 1 and 2), they would have travelled twice as fast in the conditions in which the OFG was higher (2) as compared to when OFG was lower (1). Consequently, the relation between the visual and proprioceptive information was inconsistent between trials as well as between the standard and comparison speeds. This condition will hereafter be referred to as the  $VP_{incon}$  condition.

In condition 3, subjects did not pedal the bike but instead experienced the movement trajectory by operating a computer mouse and viewing the corresponding visual image through the HMD. This condition, in which only visual cues were available and proprioceptive cues were absent, will hereafter be referred to as the V condition. The duration of each motion trajectory (both standard and comparison) was 3 sec. The optic flow patterns experienced in the V condition were equivalent to those experienced in the  $VP_{incon}$  condition.

In condition 4, only proprioceptive cues were available. In this condition, the proprioceptive input that was experienced was the same as that experienced in the  $VP_{con}$  condition, with the exception that subjects essentially pedalled in the dark, receiving no visual information from the HMD. This condition will hereafter be referred to as the P condition.

## RESULTS

The psychometric function, derived from the data from the  $VP_{con}$  condition, serves as an example of a typical function observed across all conditions (Fig. 2). Each data point represents, on average, the proportion of trials that subjects judged the comparison speed to be faster than the standard speed. The data were then fit to a psychometric function based on a probit analysis.<sup>24</sup> When the comparison speed was a great deal faster than the standard speed, subjects were more likely to judge the comparison speed as being faster. Conversely, when the comparison speed was a great deal slower than the standard speed, subjects were more likely to judge the comparison speed as being slower. Subjects' ability to discriminate between two different speeds was reflected in the steepness of the response curve. A very steep curve would suggest that subjects were able to distinguish, quite precisely, the difference between the standard speed and the comparison speed. When evaluating subjects' ability to discriminate between two speeds, the JND (as determined by the best-fit function), was calculated by subtracting the speed required to achieve 75% accuracy, from that required to achieve

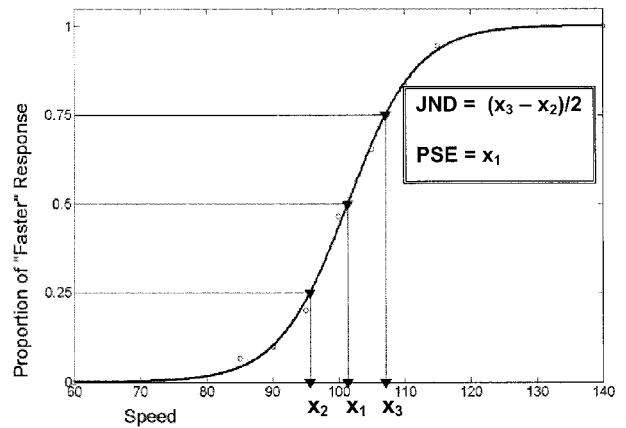


FIG. 2. An example of a typical best-fit psychometric function. Each data point represents the proportion of "comparison speed faster" responses plotted against the trial-to-trial variations in pedalling speed.

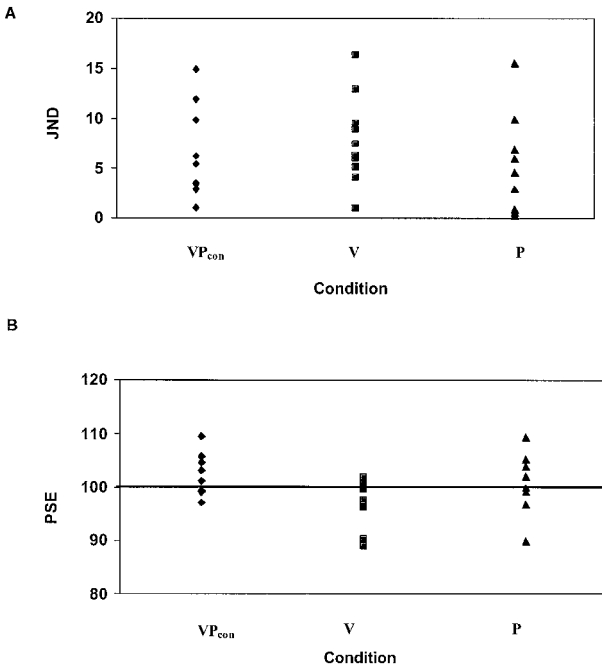
25% accuracy and dividing this value by two.<sup>25</sup> The JND represents the degree to which the comparison speed must differ from the standard speed in order for a subject to correctly discriminate the two. In addition, the point of subjective equivalence (PSE) is defined as the point at which the comparison speed was judged to be faster 50% of the time (Fig. 2).

### Manipulation of cue availability

A total of 30 subjects were tested in conditions  $VP_{con}$ , V, and P ( $VP_{con}$ , 5 males and 4 females; V, 6 males and 6 females, and P, 5 males and 4 females). Separate psychometric functions for each of the individual subjects were generated and the JNDs and the PSEs were then calculated based on each subject's psychometric function.

The distribution of the JNDs were generated from the psychometric functions for each individual subject and for each of the three conditions (Fig. 3A). High variability was observed among subjects within each condition. The mean JNDs for the  $VP_{con}$ , V, and P conditions were 6.6, 7.4, and 5.3, respectively. A between group two-factor ANOVA (3 conditions  $\times$  2 sexes) conducted on the mean JNDs was found to be not significant for either condition ( $F(2,24) = 0.59, p > 0.05$ ) or sex ( $F(1, 24) = 0.47, p > 0.05$ ). This result suggested that the discrimination thresholds were comparable regardless of whether visual and proprioceptive cues were presented alone or in combination.

The distribution of the PSEs was also generated from the psychometric functions for each individual subject and for each of the three conditions (Fig. 3B). High variability was observed among subjects



**FIG. 3.** The distribution of JNDs (A) and PSEs (B) obtained from the psychometric functions of individual subjects across three conditions: vision and proprioception combined and congruent, vision only, proprioception only.

within each condition. The mean PSEs for the VP<sub>con</sub>, V, and P conditions were 102.1, 95.7, and 103.0, respectively. A between-group two-factor ANOVA (3 conditions  $\times$  2 sexes) conducted on the mean PSEs was found to be significant for condition ( $F(2,24) = 4.54, p < 0.05$ ) but not for sex ( $F(1, 24) = 1.35, p > 0.05$ ). This result suggested that there was a difference across the three conditions in terms of which comparison speeds were perceived as being equal to the standard speed of 100. In the V condition, subjects tended to perceive the slower comparison speed (95.7) as being equal to the standard speed of 100. In other words, there was an underestimation of the standard speed when only visual information was presented. This formed a contrast to the other two conditions (VP<sub>con</sub> or P) in which a small overestimation was observed.

*Manipulation of OFG during the VP<sub>incon</sub> condition*

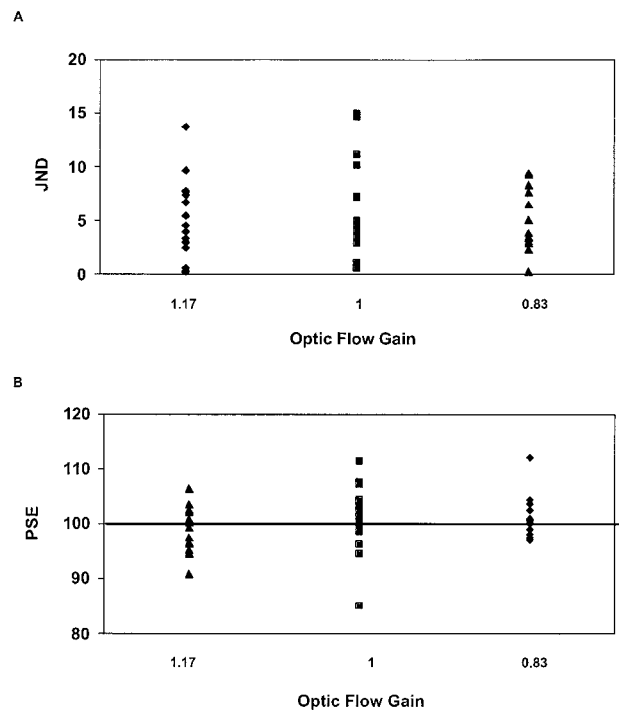
In the VP<sub>incon</sub> condition, although both visual and nonvisual information were available, OFG was randomly varied among three levels (1.17, 1, and 0.83), thus causing the relation between these two sources of sensory information to be inconsistent. In this case, if visual information played a role, dif-

ferent OFGs should result in psychometric functions that were separated along the horizontal axis. Such a separation can be revealed by comparing the PSE corresponding to each OFG.

Hypothetical PSE values can be predicted for conditions in which visual or proprioceptive cues were the only sources of information. If proprioceptive cues were the only source of information, the PSE should remain the same regardless of OFG variations. If visual cues were the only source of information, then the PSE should differ according to the corresponding OFG variations. The PSEs should form an inverse relation with the corresponding OFG values. In other words, for faster OFGs, subjects should have smaller PSE. For example, if a PSE of 100 was observed for an OFG of 1, this would mean that a PSE of 86 should be observed for an OFG of 1.17, and likewise, a PSE of 120 should be observed for an OFG of 0.83.

A total of 20 subjects were tested (6 males and 14 females) for the VP<sub>incon</sub> condition, and all subjects experienced three different OFGs. Figures 4A and 4B illustrate the distribution of subjects' JNDs and PSEs respectively as determined by the psychometric functions for each subject for all three OFG values.

High variability was found among subjects for each condition. The mean JNDs for OFGs of 1.17, 1,



**FIG. 4.** The distribution of JNDs (A) and PSEs (B) obtained from the psychometric functions of individual subjects across optic flow gains variations: 1.17, 1, and 0.83.

and 0.83 were 5.1, 6.0, and 4.7, respectively. A two-factor ANOVA (3 OFGs within group  $\times$  2 sexes) was conducted on the mean JNDs. No significant differences were found either for condition ( $F(2, 36) = 0.45, p > 0.05$ ) or sex ( $F(1, 36) = 0.18, p > 0.05$ ), thus suggesting that the discrimination thresholds were comparable across OFGs.

As predicted, higher OFGs tended to result in smaller PSEs. The mean PSEs across 20 subjects were 98.2, 101.2, and 102.1 for OFGs of 1.17, 1, and 0.83, respectively. A two-factor ANOVA (3 OFGs within group  $\times$  2 sexes) was conducted on the mean PSEs. A significant difference was found between OFG levels ( $F(2, 36) = 6.2, p < 0.01$ ), indicating that visual information played an important role. There was no significant difference between sex ( $F(2, 36) = 1.3, p > 0.05$ ).

Although the PSE analysis indicated that subjects used visual cues for estimation, the influence of vision was small. If subjects only relied on visual cues, the PSE for OFG values of 1.17 and 1 would theoretically be 86 and 100, respectively (a difference of 14% of 100). Our results showed the PSE for OFG values of 1.17 and 1 to be 98.2 and 101.2 respectively (a difference of 3% of 101.2). Therefore, subjects' reliance on visual cues for speed estimation represented 21% (3% divided by 14%) of the theoretical amount if subjects have relied on visual cues alone. In other words, visual cues contributed 21%, while proprioceptive cues contributed 79% to subject's performance. The visual contribution calculated from the comparison of PSEs for OFG values of 1 and 0.83 was smaller (4.5%).

## DISCUSSION

These results provide insight into the role of visual and proprioceptive information in estimating speed of self-motion in a number of ways. First, the manipulation of cue availability demonstrated that, regardless if visual and proprioceptive cues were provided separately or in combination, speed discrimination thresholds were comparable. This suggests that either visual or nonvisual cues alone are sufficient for speed discrimination. Although there was a high degree of variability between subjects, the threshold values were generally small, indicating that subjects were capable of performing the task.

When the relation between visual and proprioceptive information was made inconsistent by varying OFG, the resulting psychometric functions were separated along the horizontal axis. The small degree of separation between the psychometric functions corresponding to different OFGs indicated

that, although proprioceptive cues were dominant, optic flow also had a reliable effect on speed discrimination. There were no sex differences observed in any of the manipulations in this study.

### *Optic flow and speed estimation*

The role of optic flow in locomotion has been studied from a number of different perspectives. A large body of research has examined the influence of optic flow on speed estimation in visually simulated self-motion, through magnitude estimation<sup>11</sup> as well as through the detection of changes in movement speed.<sup>13</sup>

Mestre<sup>12</sup> examined speed discrimination thresholds resulting from visually simulated self-motion. It was found that subjects were able to discriminate between speeds that differed by 10%. The V condition in the current study could be considered analogous to Mestre's task and the JNDs observed in our V condition (mean = 7.4%) were consistent with Mestre's findings. Discrimination thresholds for scenarios in which both visual and proprioceptive cues are available and consistent ( $VP_{con}$ ), as well as scenarios in which proprioceptive cues are presented alone (P), have not been reported elsewhere.

One of the earliest studies to isolate the effect of optic flow on locomotion was conducted using animals (gerbils).<sup>8</sup> During the animal's target directed locomotion, optic flow was selectively manipulated and static visual cues were held constant. It was found that the animals modulated their running speed as a function of the optic flow manipulation. More recent studies on human locomotion have experimentally manipulated optic flow using elaborate setups. Often, treadmills are combined with large projection screens to present subjects with optic flow information that is yoked to their walking movement.<sup>16,17</sup>

Prokop et al.<sup>16</sup> 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 suggested that subjects modulated their movements as a result of the variations in optic flow magnitude. However, the degree to which subjects modified their movements was far less than predicted should subjects had relied only on optic flow. Overall, this study suggested that both visual and proprioceptive information play a role in modulating self-motion—findings that are relatively consistent with other studies.<sup>18,19</sup> Our study employed a different approach, in which subjects had to actively vary their speed of movement. This is in contrast to the aforementioned treadmill studies in which the subjects' task was to simply

maintain a constant movement speed. In our task subjects were required to produce a speed estimate, while in the treadmill studies, subject's walking speed was the measured response. Interestingly, these two types of paradigms produced similar results. In combination, these studies highlight the significant and often dominant role of proprioceptive information, while acknowledging the importance of optic flow.

#### *Relative weighting between visual and nonvisual cues*

The proprioceptive dominance found in the current speed discrimination task is in contrast to the results found in a traversed distance estimation task using the same experimental setup.<sup>26</sup> In the distance estimation experiment, OFG was manipulated while pedalling speed was held constant throughout the experiment. Subjects' distance estimations relied mainly on OFG rather than proprioceptive information.

Our results are consistent with the general ideas specified by the statistically optimal integration model that has recently received convincing support from work on visual-haptic integration,<sup>27-29</sup> as well as work on the integration of different cues in depth perception.<sup>30,31</sup> 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 sources. Findings from the current study seem to be consistent with this model in a number of respects. The differences observed in the relative weighting of visual and proprioceptive cues found in speed estimation and distance estimation could be partly due to both the nature of the task (distance vs. speed) and/or the perceived reliability of each cue. Whereas speed information can be obtained from cues available at a particular instance, traversed distance estimation requires the integration of information over time. During our speed estimation task, because subjects were responsible for varying their own movement speed, this may have caused them to disproportionately attend to proprioceptive information as compared to the simultaneously experienced optic flow information. Therefore, subjects may have perceived the proprioceptive information to be more reliable than the visual information. In contrast, in the aforementioned distance estimation task, subjects pedalled the bike at a comfortable, constant speed and thus only slight effort was required to track their pedalling movements. This would not have caused subjects to attend more closely to the proprioceptive cues. However, because OFG was the only cue being manipulated, this may have led subjects to attend more

closely to visual information. Therefore, in the distance estimation task, subjects may have perceived the visual information as being more reliable than the proprioceptive information. It is therefore conceivable that speed estimation task and distance estimation task may result in differences in cue weighting.

#### *VR as a tool for sensory and spatial research*

When examining the separate contributions of different sources of information from different modalities, one approach researchers can take involves developing experimental paradigms in which information from individual sources can be manipulated independently. VR is an ideal candidate for implementing such an experimental design. Although what this essentially involves is creating an artificial laboratory manipulation, the overall design of the task should still remain ecologically valid. Although the conflict that results may be contrived, the goal is to understand the natural interactions that occur between humans and their environments. Indeed, apart from studies that implement perceptual conflicts for the purpose of studying multisensory interactions, the purpose of VR is more often to simply simulate real world experiences. One of the main applications for VR in psychological research is to study spatial learning and spatial memory as obtained through navigation.

When evaluating the degree to which a VR simulation resembles its real world counterpart, two aspects should be considered: the degree to which the sensory information presented is perceptually similar to its real world counterpart and the extent to which the VR interface allows users to interact with an environment in a way that is similar to the real world.<sup>32</sup>

The visual presentation devices included in VR set-ups can range from simple desktop displays (monitors), to systems equipped with HMDs, to stereoscopic projection systems with multiple screens (e.g., CAVE). In addition, high quality visual images of an environment, including rich textural information allows observers to update their movement effectively using optic flow information and to transfer the spatial knowledge gained from a symbolic representation into knowledge that approximates real world experiences.<sup>33</sup> Different types of displays result in different levels of immersion and thus different levels of "presence."

VR can potentially integrate various modes of physical or motor input with a computer-generated environment. In order to accomplish this, the VR setup must incorporate information from participants' movements, while simultaneously provid-

ing concordant visual and nonvisual feedback resulting from this movement. The most commonly used input devices are keyboards, mouses, and joysticks.<sup>34</sup> These devices allow the participants viewpoint to undergo both translations and rotations by updating the visual information they receive accordingly. However, in these scenarios idiothetic information about self-motion is not available. Advanced setups however are able to infer both translational and rotational information directly from subjects' body movements.<sup>2,3,35</sup> These devices allow users to interact with the virtual environment in a more natural way.

One way to assess the quality of a VR simulation compared to real world navigation would be to compare spatial learning following navigation in each. Such comparisons could also be made between VR setups that differ in terms of the types of interfaces they are comprised of.

Researchers have assessed the accuracy with which participants are able to point to or move towards previously learned targets. Participants appear to be significantly more accurate and more consistent in real-world conditions than in other conditions not involving natural movement.<sup>32,36,37</sup> Chance et al.<sup>2</sup> found that, when a visual display was updated in response to full body movements, spatial knowledge acquisition was facilitated in comparison to conditions in which this updating was not possible.

We have compared spatial performance following real world navigation to performance following navigation in a virtual environment using both a bicycle interface and an interface that allows one to navigate via computer mouse. We found comparable performance for real-world navigation and VR bicycle navigation; however, spatial performance following VR mouse navigation was much poorer.<sup>38</sup> This increase in performance due to the addition of higher levels of proprioception (i.e., pedalling movements) compared to lower levels of proprioception (i.e., hand movements) has also been demonstrated in a distance estimation task.<sup>26</sup>

Another way to assess whether a VR interface sufficiently simulates natural sensory interactions is to examine the extent to which different sources of information are accurately calibrated with each other. This can, to some extent, be detected by assessing the degree of cybersickness experienced by subjects during the task. When different sources of sensory information are not well calibrated, cybersickness can potentially result.<sup>39</sup> For instance, when the visual presentation of self-motion is presented in the absence of physical movement information,

particularly when the movement includes the entire visual scene, motion sickness will be more likely to occur. Even when all sources of information are available simultaneously, they should occur in synchrony and should be matched in space and time. If there is a temporal delay or lag that occurs when the visual scene is updated in response to participants' movements, this often results in the experience of cybersickness.

The design of our current behavioural task, as well as the properties of our interface, has allowed us to overcome problems related to cybersickness. Our setup allows different sources of important sensory information to be present at once (both visual and proprioceptive). This information is fed into a high-end SGI graphics computer, capable of updating the visual display with minimal delay, which is paired with a HMD, and high-speed signal acquisition hardware device. Moreover, the task described in the current study simply involves translational movements in a straight, empty hallway and requires no rotational movements. The forward visual flow field experienced is tightly yoked to the pedalling movements. Although in the  $VP_{incon}$  condition OPGs were varied slightly between trials, OFG remained the same within any given trial.

Although we did not use a standardized scale to measure cybersickness, we did informally ask subjects to rate the degree of sickness they experienced during the experiment (e.g., headaches, nausea, light-headedness) on a scale from one to five (with five being most severe). Practically all subjects gave ratings on the lower end of the scale (1–2) indicating that they experienced very little cybersickness throughout the experiment. Further, subject ratings did not differ as a function of condition, indicating that the "conflict" condition (i.e.,  $VP_{incon}$ ) did not induce a greater degree of cybersickness than did non-conflict conditions (i.e.,  $VP_{con}$ ).

In summary, VR technology has emerged as an invaluable tool that maintains the ability to create experimental manipulations that cannot be accomplished in the real world, while remaining an ecologically valid testing paradigm. By developing a novel VR paradigm, the current study is the first to investigate the relative contributions of visual and proprioceptive information in speed discrimination during self-motion. It is also one of the few studies to investigate the relative contributions of different sensory cues in locomotion in general. Ultimately, this paradigm has allowed us to gain further insight into the underlying neural mechanisms responsible for integrating different sources of sensory information.

## ACKNOWLEDGMENTS

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Address reprint requests to:

Dr. Hong-Jin Sun  
Department of Psychology  
McMaster University  
1280 Main Street West  
Hamilton, ON, Canada, L8S 4K1

E-mail: sunhong@mcmaster.ca

