# Research Article

# Visual Control of Action Without Retinal Optic Flow

Jack M. Loomis, Andrew C. Beall, Kristen L. Macuga, Jonathan W. Kelly, and Roy S. Smith

<sup>1</sup>Department of Psychology and <sup>2</sup>Department of Electrical and Computer Engineering, University of California, Santa Barbara

ABSTRACT—In everyday life, the optic flow associated with the performance of complex actions, like walking through a field of obstacles and catching a ball, entails retinal flow with motion energy (first-order motion). We report the results of four complex action tasks performed in virtual environments without any retinal motion energy. Specifically, we used dynamic random-dot stereograms with single-frame lifetimes (cyclopean stimuli) such that in neither eye was there retinal motion energy or other monocular information about the actions being performed. Performance on the four tasks with the cyclopean stimuli was comparable to performance with luminance stimuli, which do provide retinal optic flow. The near equivalence of the two types of stimuli indicates that if optic flow is involved in the control of action, it is not tied to first-order retinal motion.

The contributions of J.J. Gibson to the understanding of visually controlled action are legend. Most important are his formulations of the optic array (variation in light flux with different visual directions) and optic flow (changes in the optic array produced by movements of the observer; Gibson, 1950, 1958), his recognition of the importance of optic flow in informing the observer of self-motion (Gibson, 1958), the first mathematical specification of optic flow (Gibson, Olum, & Rosenblatt, 1955), and his identification of different spatial behaviors that might be controlled using various aspects of optic flow (Gibson, 1958, 1979). Since his seminal work, innumerable studies have taken up where he left off. These research efforts include more general mathematical specifications of optic flow and its processing (e.g., Beintema, van den Berg, & Lappe, 2004; Gordon, 1965; Heeger & Jepson, 1992; Prazdny, 1980; Royden, 2004), iden-

Address correspondence to Jack Loomis, Department of Psychology, University of California, Santa Barbara, CA 93106-9660, e-mail: loomis@psych.ucsb.edu.

tification of additional spatial behaviors that rely on optic flow (e.g., Loomis & Beall, 1998; Warren, 1998), psychophysical research on the perception of self-motion using optic flow (e.g., Crowell & Banks, 1993; Cutting, Springer, Braren, & Johnson, 1992; Warren, Morris, & Kalish, 1988), and the investigation of running and walking, driving, flying, and ball catching using active control tasks (e.g., ball catching: McBeath, Shaffer, & Kaiser, 1996; driving: Godthelp, 1986; Land, 1998; Wann & Wilkie, 2004; flying: Beall & Loomis, 1997; running and walking: Patla, 2004; Warren & Fajen, 2004). In addition, Gibson's ideas have stimulated research on visually controlled behavior in nonhuman species (e.g., Frost & Sun, 1997; Lee, 1998; Srinivasan, 1998) and efforts to identify the physiological mechanisms involved in the processing of optic flow as it relates to control of locomotion (e.g., Frost & Sun, 1997; Raffi & Siegel, 2004; Wylie & Frost, 1999).

Because optic flow usually arises from the observer's movement through an environment of visually distinct points, contours, and surfaces, optic flow inevitably entails retinal flow with motion energy (Adelson & Bergen, 1985). Optic flow is usually defined in terms of a head-centered reference frame and therefore does not depend on eye rotations; in contrast, eye rotations cause retinal motions and, thus, alter the correspondence between retinal and optic flow. As a consequence, the processing of optic flow is usually thought to depend on the sensing of both retinal flow and nonretinal signals specifying eye and head rotations. Yet because optic flow almost always entails retinal flow, research on the physiology of optic-flow processing has invariably been concerned with retinal motion (with first-order motion energy), as opposed to less common and weaker forms of visual motion—so-called second-order and third-order motion (Lu & Sperling, 2002).

Yet from very early on, Gibson (1958) intended that optic flow not be too closely identified with retinal flow, in part because of the complexity of retinal motion produced by eye rotations. By defining the optic array in terms of projections of the surrounding visible environment, and by defining optic flow as changes in the optic array associated with observer movement, he left open the possibility that optic flow might be signaled by mechanisms other than those acting upon first-order retinal flow.

Here we show that various complex actions are possible with a stimulus that lacks retinal optic flow but nevertheless has optic flow in the more abstract sense. This stimulus is the now-classic cyclopean motion stimulus, defined by a succession of randomdot stereograms that are uncorrelated from one frame to the next. That is, each frame of the motion stimulus begins with a new random-dot pattern, and the two binocular images for each frame differ by a binocular disparity signal conveying information about shape in depth. Each eye views scintillating noise over time, but a person with normal stereopsis experiences a dynamic moving stimulus defined by variations in stereoscopic depth. Julesz (1971) first reported creating and using such a cyclopean stimulus to study motion in the frontoparallel plane. Since then, many other researchers have used this cyclopean stimulus to investigate questions about motion perception both in the frontoparallel plane and in depth (for review, see Patterson, 1999). Gray and Regan (1996) were the first to apply the cyclopean stimulus to the investigation of optic flow in connection with action. They demonstrated that people are quite accurate at judging time to contact of an approaching stimulus on the basis of optical expansion of a stereo-defined object. In a recent examination of heading perception (Macuga, Loomis, Beall, & Kelly, in press), we simulated observer motion parallel to a ground surface covered with either cyclopean-defined or luminance-defined objects and found that heading perception with the cyclopean stimulus was nearly as good as heading perception with a luminance-defined stimulus.

In the work reported here, we took advantage of a novel technique for creating cyclopean stimulation developed by the second author. Because the technique involves real-time computer graphics using special-purpose software in conjunction with 3-D graphics hardware, the flexibility of the technique allows us to create active control tasks in which the 3-D graphics model used in rendering the cyclopean stimulus is modified in accordance with the observer's actions. In particular, using an immersive virtual-reality system with a head-mounted display (HMD), participants are able to move around within a virtual environment conveyed only by cyclopean stimulation.

As other researchers, beginning with Julesz (1971), have noted, it is remarkable that people can see moving objects conveyed only by cyclopean stimulation, given that the visual system has to establish the binocular correspondence between the two random-dot patterns with lifetimes of only one graphics frame (typically, 17 ms) and then build up a 3-D representation based on the recovered disparities. Most participants immediately perceive the virtual environment in which we place them, but a few require up to 30 s. Once participants "tune in" to the virtual environment, they immediately can begin to interact effortlessly with objects of interest. Here we report the results obtained with four visually controlled actions that required the

participants to move around quickly and accurately while interacting with stationary and moving objects. The results indicate that performance with cyclopean stimulation is comparable to performance with luminance stimulation. The fact that participants require no specific training and very little practice with these tasks using the cyclopean stimulation means that it provides some of the same action-related information afforded by luminance stimulation, which includes retinal optic flow and monocular depth cues.

#### **METHOD**

# Equipment and Stimuli

The type of virtual-reality system used in this study was initially developed in our laboratory and has since been used in many other research projects at the University of California at Santa Barbara. Participants' head orientation was measured with a three-axis orientation sensor (Intersense IS300). Position of the head was tracked in 3-D by a four-camera video tracking system (Worldviz PPT ×4) capable of measuring position with a resolution of better than 1 mm throughout the work space, which measured 4 m by 7 m. The delay between head motion and display update was 42 ms. Projectively correct stereoscopic images were rendered by a 3.0-GHz computer with an nVidia Geforce 6800 graphics card. All stimuli were presented with a Virtual Research V8 HMD with two LCD panels that were refreshed at 60 Hz and had a resolution of 640 × 480 pixels; the graphics images were also updated at 60 Hz for both displays. Field of view for each display was 50° horizontal by 38° vertical, with 100% binocular overlap. The simulated interpupillary distance was 6 cm for all participants.

The different virtual environments used in this work were created with 3-D modeling tools (3D Studio Max and in-house software). The sizes and shapes of objects and surfaces were tessellated and rendered with polygons. The virtual environment was thus defined by the positions and orientations of the surfaces and objects. Participants walking around in the simulated environments experienced a strong sense of "presence" within the environments.

All 3-D environments (including interactive immersive ones) that are implemented with graphics cards supporting the OpenGL graphics library can be displayed by way of the cyclopean stimulus using custom software (source code available on the Web at http://www.recveb.ucsb.edu/stickydots.htm). At a 60-Hz graphics update rate in each eye, the software casts up to 1,000 white random dots onto the surfaces of the virtual environment within the observer's field of view. Perspective images of these 1,000 dots, rendered separately for the two eyes, are then sent to the corresponding visual displays. The 1,000 dots are spread over the field of view with constant angular density against a black background. When the cast dots have only single-frame lifetimes, each eye is exposed to a scintillating field of uniform dot density. Binocular viewing, however, allows

a person to perceive a 3-D environment populated with surfaces and objects, some of which may be moving. Because convergence and binocular disparity are the sole basis for perceiving the virtual environment, only variations in egocentric distance across the visual scene have the possibility of being seen. Thus, variations in lightness, color, and texture within the conventionally rendered virtual environment are invisible. Also, because the HMD we used has a horizontal pixel spacing of 4.5 min of arc, the rather low display resolution and the sparse density of dots defining small distant objects limited their visibility. When trying out a borrowed HMD with double the vertical and horizontal display resolution, we observed that objects could be seen at greater simulated distances.

## Participants

The 12 participants were all undergraduates who received course credit. Eight participated in the main experiment, 2 in the first control experiment, and 2 in the second control experiment. All had at least 20/20 visual acuity and 70% stereopsis, as measured by a Keystone Orthoscope. In addition, while wearing the HMD, all correctly reported a three-digit number defined by the cyclopean stimulus. All were unaware of the purpose of the research and had no experience with dynamic cyclopean stimulation.

#### Tasks

The four tasks were ball catching, ground interception, obstacle avoidance, and path following. For each, the primary comparison of interest was between binocular luminance stimulation and cyclopean stimulation. Because we also included a control condition in which one eye was blocked while the other viewed the cyclopean stimulus, we refer to the two cyclopean conditions as binocular cyclopean and monocular cyclopean.

In the ball-catching task (Figs. 1a, 1b, and 1d), balls 25 cm in diameter were launched from a visible launch box on the ground 5 m from the origin, which was used as the initial observation point on all trials. The balls were launched with an initial vertical velocity of 7 m/s and varying direction and horizontal velocity such that the landing point was always within a rectangular area (2 m from side to side and 1 m deep) centered on the origin. They were accelerated downward by a reduced gravity of 4.8 m/s<sup>2</sup> and arrived close to the participant's location within about 2.5 s; flight time was always 2.9 s when the ball was not caught. The participant tried to "catch" each ball with the forehead (like a "header" in soccer). If the center of the participant's head was within the ball's radius, the trial was scored as successful, and the participant heard an appropriate signal. After each trial, the participant walked back to the origin. The virtual environment, including the origin, was always rendered as luminance stimulation during this return phase to permit the

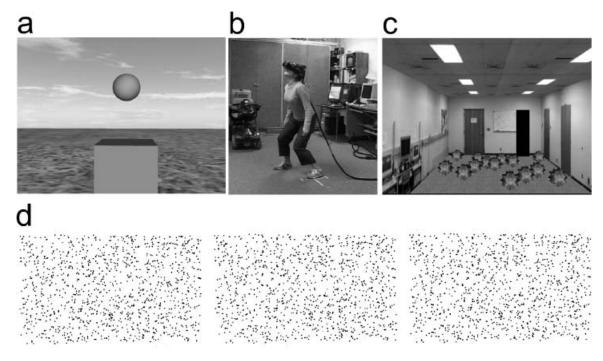


Fig. 1. Depiction of the ball-catching and obstacle-avoidance tasks. The single graphics frame in (a) shows the ball leaving the launch box in the luminance condition of the ball-catching task. The depicted field of view is slightly narrower than that experienced by the participant. The illustration in (b) shows the third author performing this task. The stimuli shown in (d) are a single graphics frame from the binocular cyclopean condition of this task and again show the ball leaving the launch box. The cyclopean stimulus was viewed stereoscopically in the head-mounted display, but the images depicted here are for free fusion, left pair for crossed viewing and right pair for uncrossed viewing. A single graphics frame from the obstacle-avoidance task is shown in (c). The goal was the black rectangle at the far end of the rendered room.

return even when there was no useful visual stimulation during the action phase. The next trial began 2 s later.

The ground-interception task was similar, except that the balls (15 cm in diameter) moved at constant horizontal velocity over the ground from the visible launch box (2 m from the origin, which was the initial observation point). Over trials, launch direction varied from  $-42^{\circ}$  to  $49^{\circ}$  (the origin was at  $0^{\circ}$ ), but did not include directions within  $11^{\circ}$  of the origin, and horizontal velocity varied from  $0.8\,\mathrm{m/s}$  to  $1.77\,\mathrm{m/s}$ . Participants walked to intercept the ball before it crossed a line behind the origin. A tone signaled successful interception (when the vertical projection of the observer's head was within the ball's radius). After each trial, the participant walked back to the origin. The virtual environment, including the origin, was always rendered as luminance stimulation during this return phase. The next trial began  $2\,\mathrm{s}$  later.

In the obstacle-avoidance task, the participant attempted to walk from the origin to a rectangular goal target (2 m high) placed at the far wall of the virtual room (5 m away). The participant walked through a field of 14 star-shaped obstacles (50 cm wide) placed on the ground on the near side of the goal (see Fig. 1c). This task is like that studied by Fajen and Warren (2003). There were 10 different configurations of target and obstacles used as stimuli. Lateral placement of the goal was varied, and placement of the obstacles was quasi-random such that there was always at least one obvious path to the goal. Participants viewed the configuration and then immediately began walking to the goal while attempting to avoid hitting obstacles. If the horizontal position of the head was within 25 cm of an obstacle, this was scored as a collision, and a sound informed the participant. Upon reaching the goal, the participant returned to the origin, with rendering of the environment always done by luminance stimulation. Performance was scored in terms of number of obstacle collisions and travel time to the goal.

The path-following task was to follow a path defined by an object moving in a horizontal plane. At the beginning of each trial, the participant viewed a train of four spheres, each 7.5 cm in radius, resting on a horizontal plane 0.84 m below eve level. The balls were spaced 15 cm apart so that the spheres just barely touched. Once a trial was under way, the spheres moved together along a circuitous path through a space measuring  $2 \times 3$  m. They moved with a forward velocity of 0.3 m/s and turned with a maximum turn rate of 60°/s. The spheres' trajectories were prerecorded by the experimenter. Participants were instructed to stay close to the fourth sphere in the train, acting as though they were the fifth sphere (like a caboose). Performance was measured as the root mean square (rms) error between the center of the head, projected onto the lower plane, and the center of what would have been the fifth ball. Luminance stimulation guided the participant back to the origin for the next trial.

#### Procedure

Upon arrival for the experiment, participants had their vision tested. In the main experiment, the order of the four tasks was

counterbalanced. For each task, the binocular luminance and binocular cyclopean conditions were performed as blocks, with counterbalancing across participants. For ball catching, 15 practice trials preceded the 30 test trials in each condition; the corresponding values were 6 practice and 20 test trials for ground interception and 4 practice and 10 test trials for obstacle avoidance. For each task and condition, practice lasted about 1 min. For each condition of the path-following task, participants were given 30 s of practice followed immediately by 90 s of testing. After completing all four tasks in both conditions, participants were assigned at random to one of the four tasks and attempted to perform it with an eye patch over one eye while they viewed the cyclopean stimulus (monocular cyclopean condition). Thus, each of the four tasks in the monocular cyclopean condition was performed by 2 of the 8 participants. This last part of the experiment was conducted to check for monocular artifacts in the cyclopean stimulus. Because participants reported seeing nothing in this condition, they experienced the task as a meaningless activity even though they were sometimes successful in the two interception tasks by chance alone.

Two control experiments were conducted after the main experiment. In the first, 2 participants performed the four tasks with the monocular cyclopean stimulus and then with the stimulus turned off during task execution (no-vision condition). For each task and condition, they received approximately 1 min of practice with the binocular cyclopean stimulus (to be familiarized with the task), 1 more min of practice with the monocular cyclopean stimulus or with no vision, and then the test phase (same as practice). Thus, the results for the monocular cyclopean stimulus for each task were based on 4 participants (2 from the main experiment and 2 more from the first control experiment), and the results for no vision for each task were based on just 2 participants. In the second control experiment, 2 participants performed the four tasks with the binocular luminance and monocular luminance stimuli. The purpose of this experiment was to determine whether performance with luminance stimuli improved when binocular information was added to monocular information.

## RESULTS

The upper panels of Figure 2 give the recorded trajectories in the obstacle-avoidance task for 1 of the 10 configurations in three of the conditions. The lower panel gives the mean number of obstacles hit in each condition. The values were slightly lower for binocular luminance than for binocular cyclopean, t(7) = -2.701, p < .05; d = 0.955. We did not test for other comparisons because of unequal sample sizes, but the pattern is clear: The binocular luminance and monocular luminance conditions show comparable levels of control, and the monocular cyclopean and no-vision conditions show the same poor performance, indicating that no usable artifact was present in the monocular cyclopean stimulus. The other performance measure for this

# Obstacle Avoidance Task

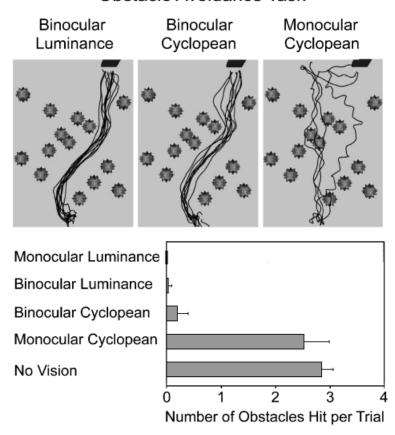


Fig. 2. Results of the obstacle-avoidance task. The upper panels give plan views of the walking trajectories for all participants for 1 of the 10 configurations in the binocular luminance, binocular cyclopean, and monocular cyclopean conditions, respectively, from left to right. Fewer participants performed in the latter condition. The lower panel gives the mean number of obstacles collided with per trial in each of the five viewing conditions. Error bars represent +1 standard deviation. The comparison of primary interest is that between the binocular luminance and binocular cyclopean conditions, in which 8 participants performed.

task was time to arrive at the goal. The mean times were  $10.6 \,\mathrm{s}$  and  $14.4 \,\mathrm{s}$  for the binocular luminance and binocular cyclopean conditions, respectively, indicating slightly poorer performance with the cyclopean stimulus, t = -5.021, p < .01; d = 1.775.

Figure 3 gives the results for path following. The upper panel shows representative walking trajectories from the first 25 s of a trial in the binocular cyclopean and monocular cyclopean conditions. In the binocular cyclopean condition, the participant's path closely mirrors that of the lead stimulus, indicating visual control of locomotion. In contrast, the trajectory for the monocular cyclopean condition indicates no visual control. The lower panel gives mean rms error as a function of condition. The values for binocular luminance and binocular cyclopean were not significantly different; other comparisons were not tested because of unequal ns, but again the pattern is clear—comparable levels of visual control in three of the conditions and the absence of control in the remaining two.

Figure 4 gives the results for ball catching. The upper panel plots a measure of catching error as a function of time during the

last 2.5 s of the ball's trajectory. The measure of error is the distance between the center of the participant's head and the point at head level through which the ball eventually passed. The plots are based on all trials, including catches and misses. Clearly, performance in the monocular luminance, binocular luminance, and binocular cyclopean conditions was visually controlled and to a similar degree, whereas performance in the monocular cyclopean and no-vision conditions was not controlled. The lower panel gives another measure of performance—percentage of balls caught. The binocular luminance and binocular cyclopean conditions were not significantly different. Other comparisons were not tested (because of unequal ns), but the pattern of control apparent in the upper panel of Figure 4 is apparent here as well.

Finally, Figure 5 presents the results for ground interception. Percentage of balls intercepted is given as a function of condition. Again, the binocular luminance and binocular cyclopean conditions were not significantly different. Three conditions, monocular luminance, binocular luminance, and binocular

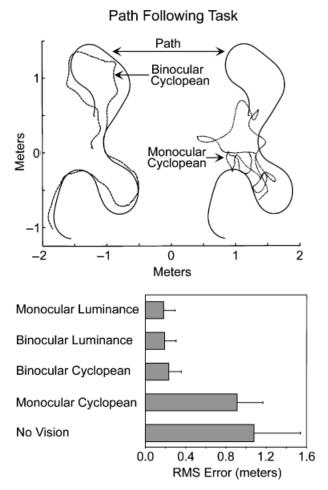


Fig. 3. Results of the path-following task. The upper panel shows representative walking trajectories from the first  $25~\rm s$  of a trial for 1 participant in the binocular cyclopean condition and 1 participant in the monocular cyclopean condition. The lower panel gives root mean square (rms) error in each of the five viewing conditions. Error bars represent +1 standard deviation. The comparison of primary interest is that between the binocular luminance and binocular cyclopean conditions, in which 8 participants performed.

cyclopean, permitted visual control at comparable levels, and the two remaining conditions led to equally poor performance, indicating that no useful artifact was present in the monocular cyclopean condition.

### DISCUSSION

Across the four tasks, performance with binocular cyclopean stimulation was comparable to performance with full-cue binocular luminance stimulation. This is an impressive result given that participants received no specific training and very little practice. Because the scintillating noise of the cyclopean stimulation in each eye had no first-order retinal motion that was correlated with the spatial layout of the environment or with the participants' action, these results show that retinal optic flow need not be the basis for visually guided action. Admittedly, our

tasks were not as challenging as many real-world tasks. The spatial and temporal bandwidth limitations of cyclopean vision (Patterson, 1999) suggest that certain tasks, like playing tennis or cricket, might be very challenging, if not impossible, with this kind of stimulation. However, we are quite impressed with how well people can see fast-moving complex objects with cyclopean stimulation. One of the primary limitations of our current implementation is that with only 1,000 white dots defining the environment in each graphics frame, small objects in the distance are rendered by only a small number of dots, making them difficult to see against the background. In the future, an implementation with many more points defining the cyclopean stimulus and an HMD with higher spatial resolution might well allow people to perform skilled actions approaching the demands of tennis and cricket.

Our control experiments establish two points. First, because performance was comparable in the monocular cyclopean and no-vision conditions, any concern that performance in the bin-

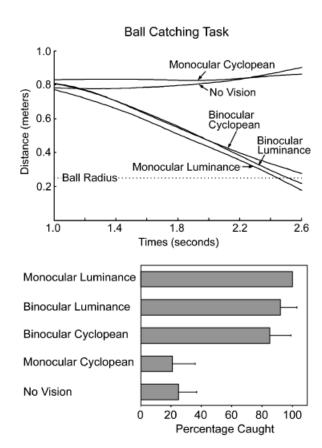


Fig. 4. Results for the ball-catching task. The upper panel plots a measure of catching error as a function of time during the last 2.5 s of the ball's trajectory. The measure of error is the distance between the center of the participant's head and the point at head level through which the ball eventually passed. The plots are based on all trials, including catches and misses. The lower panel gives mean percentage of balls caught in each of the five viewing conditions. Error bars represent +1 standard deviation. The comparison of primary interest is that between the binocular luminance and binocular cyclopean conditions, in which 8 participants performed.

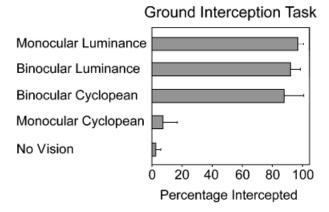


Fig. 5. Results for the ground-interception task. Percentage of balls intercepted is given for each of the five viewing conditions. Error bars represent +1 standard deviation. The comparison of primary interest is that between the binocular luminance and binocular cyclopean conditions, in which 8 participants performed.

ocular cyclopean condition might have been mediated by a monocular artifact can be dismissed. Second, the comparability of performance in the binocular and monocular luminance conditions means that binocular information was unnecessary in the performance of these particular tasks.

The finding of comparable levels of performance with the binocular cyclopean stimulus containing only binocular information, the monocular luminance stimulus containing only monocular information, and the binocular luminance stimulus containing both monocular and binocular information is consistent with two different interpretations. The first is that the observers relied only on the changing perspective information, conveyed independently by the cyclopean stimulus and by the monocular luminance stimulus. Although distance information is explicitly provided by cyclopean perception, the control of behavior need not make use of this distance information. This interpretation is consonant with Gibson's hypothesis of optic flow (in the abstract sense) as the basis for the visual control of action. The second interpretation is that the observers executed the tasks using 3-D perceptual representations that included distance (e.g., DeLucia, Kaiser, Bush, Meyer, & Sweet, 2003; Hahn, Andersen, & Saidpour, 2003; Loomis & Beall, 1998; Vishton & Cutting, 1995). Such representations are suitable for continued open-loop control if the visual stimulation is unexpectedly terminated (Loomis & Beall, 2004).

These two interpretations are not mutually exclusive. Different actions may involve one kind of information or the other, and even within an action (e.g., traveling to a goal through a field of obstacles), 3-D representations might be involved in certain phases of execution (e.g., route selection) and abstract optic flow might be involved in others (e.g., steering clear of an obstacle). The present results do not favor one interpretation over the other. As a point of interest, we have observed informally that cyclopean stimulation, like luminance stimulation, does allow for open-loop execution over short periods, a result consistent with

visual control by a 3-D representation (Loomis & Beall, 2004). Still, closed-loop performance of the four tasks, as studied here, is consistent with both control by optic flow and control by 3-D representation.

Finally, the present findings (see also Macuga et al., in press) imply that computational models of visually controlled action based solely on retinal motion processing are of limited value. Clearly, the ease and accuracy with which people can perform complex spatial actions with cyclopean stimulation signify that models of visually controlled action need to be based on more abstract properties of the visual stimulus, like abstract optic flow, or on 3-D representations resulting from either of two distinct processing streams (retinal image motion and stereopsis).

Acknowledgments—This research was supported by Grant F49620-02-1-0145 from the Air Force Office of Scientific Research. A preliminary report of this work was given at the annual meeting of the Vision Sciences Society in Sarasota, FL, May 2003. The authors thank Bill Warren for helpful criticism during the early stages of this work and Editor James Cutting for his helpful suggestions for improving the research reported here and for improving the figures. Anaglyph demonstrations of moving objects conveyed by cyclopean stimulation can be downloaded at http://www.recveb.ucsb.edu/stickydots.htm.

#### REFERENCES

Adelson, E.H., & Bergen, J.R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America A*, 2, 284–299.

Beall, A.C., & Loomis, J.M. (1997). Optic flow and visual analysis of the base-to-final turn. The International Journal of Aviation Psychology, 7, 201–223.

Beintema, J.A., van den Berg, A.V., & Lappe, M. (2004). Circular receptive field structures for flow analysis and heading detection. In L. Vaina, S. Beardsley, & S. Rushton (Eds.), *Optic flow and beyond* (pp. 223–248). Boston: Kluwer Academic.

Crowell, J.A., & Banks, M.S. (1993). Perceiving heading with different retinal regions and types of optic flow. *Perception & Psychophysics*, 53, 325–337.

Cutting, J.E., Springer, K., Braren, P.A., & Johnson, S.H. (1992).
Wayfinding on foot from information in retinal, not optical, flow.
Journal of Experimental Psychology: General, 121, 41–72.

DeLucia, P.R., Kaiser, M.K., Bush, J.M., Meyer, L.E., & Sweet, B.T. (2003). Information integration in judgements of time to contact. Quarterly Journal of Experimental Psychology: Human Experimental Psychology, 56, 1165-1189.

Fajen, B.R., & Warren, W.H. (2003). Behavioral dynamics of steering, obstacle avoidance, and route selection. *Journal of Experimental Psychology: Human Perception and Performance*, 29, 343–362.

Frost, B.J., & Sun, H.J. (1997). Visual motion processing for figure/ ground segregation, collision avoidance, and optic flow analysis in the pigeon. In M.V. Srinivasan & K. Venkatesh (Eds.), From living eyes to seeing machines (pp. 80–103). London: Oxford University Press.

220

- Gibson, J.J. (1950). The perception of the visual world. Boston: Houghton-Mifflin.
- Gibson, J.J. (1958). Visually controlled locomotion and visual orientation in animals. *British Journal of Psychology*, 49, 182–194.
- Gibson, J.J. (1979). The ecological approach to visual perception. Boston: Houghton-Mifflin.
- Gibson, J.J., Olum, P., & Rosenblatt, F. (1955). Parallax and perspective during aircraft landings. American Journal of Psychology, 68, 372–385.
- Godthelp, H. (1986). Vehicle control during curve driving. Human Factors, 28, 211–221.
- Gordon, D.A. (1965). Static and dynamic visual fields in human space perception. *Journal of the Optical Society of America*, 55, 1296– 1303.
- Gray, R., & Regan, D. (1996). Cyclopean motion perception produced by oscillations of size, disparity and location. *Vision Research*, 36, 655–665.
- Hahn, S., Andersen, G.J., & Saidpour, A. (2003). Static scene analysis for the perception of heading. Psychological Science, 14, 543–548
- Heeger, D.J., & Jepson, A.D. (1992). Subspace methods for recovering rigid motion: I. Algorithm and implementation. *International Jour*nal of Computer Vision, 7, 95–117.
- Julesz, B. (1971). Foundations of cyclopean perception. Chicago: University of Chicago Press.
- Land, M.F. (1998). The visual control of steering. In L.R. Harris & M. Jenkin (Eds.), Vision and action (pp. 163–180). Cambridge, England: Cambridge University Press.
- Lee, D.N. (1998). Guiding movement by coupling taus. Ecological Psychology, 10, 221–250.
- Loomis, J.M., & Beall, A.C. (1998). Visually-controlled locomotion: Its dependence on optic flow, 3-D space perception, and cognition. *Ecological Psychology*, 10, 271–285.
- Loomis, J.M., & Beall, A.C. (2004). Model-based control of perception/ action. In L. Vaina, S. Beardsley, & S. Rushton (Eds.), Optic flow and beyond (pp. 421–441). Boston: Kluwer Academic.
- Lu, Z.L., & Sperling, G. (2002). Stereomotion is processed by the thirdorder motion system: Reply to comment on "Three-systems theory of human visual motion perception: Review and update." *Journal* of the Optical Society of America A, 19, 2144–2153.
- Macuga, K.L., Loomis, J.M., Beall, A.C., & Kelly, J.W. (in press). Perception of heading without retinal optic flow. *Perception & Psychophysics*.

- McBeath, M.K., Shaffer, D.M., & Kaiser, M.K. (1996). On catching fly balls. Science, 273, 256–260.
- Patla, A.E. (2004). Gaze behaviors during adaptive human locomotion: Insights into how vision is used to regulate locomotion. In L. Vaina, S. Beardsley, & S. Rushton (Eds.), Optic flow and beyond (pp. 383–399). Boston: Kluwer Academic.
- Patterson, R. (1999). Stereoscopic (cyclopean) motion sensing. Vision Research, 39, 3329–3345.
- Prazdny, K. (1980). Ego motion and relative depth map from optical flow. *Biological Cybernetics*, 36, 87–102.
- Raffi, M., & Siegel, R.M. (2004). Multiple cortical representations of optic flow processing. In L. Vaina, S. Beardsley, & S. Rushton (Eds.), Optic flow and beyond (pp. 3–22). Boston: Kluwer Academic.
- Royden, C.S. (2004). Modeling observer and object motion processing. In L. Vaina, S. Beardsley, & S. Rushton (Eds.), *Optic flow and beyond* (pp. 159–181). Boston: Kluwer Academic.
- Srinivasan, M.V. (1998). Insects as Gibsonian animals. Ecological Psychology, 10, 251–270.
- Vishton, P.M., & Cutting, J.E. (1995). Wayfinding, displacements, and mental maps: Velocity fields are not typically used to determine one's aimpoint. *Journal of Experimental Psychology: Human Perception and Performance*, 21, 978–995.
- Wann, J.P., & Wilkie, R.M. (2004). How do we control high speed steering? In L. Vaina, S. Beardsley, & S. Rushton (Eds.), Optic flow and beyond (pp. 401–420). Boston: Kluwer Academic.
- Warren, W.H. (1998). Visually controlled locomotion: 40 years later. Ecological Psychology, 10, 177–219.
- Warren, W.H., & Fajen, B.R. (2004). From optic flow to laws of control. In L. Vaina, S. Beardsley, & S. Rushton (Eds.), Optic flow and beyond (pp. 307–337). Boston: Kluwer Academic.
- Warren, W.H., Morris, M.W., & Kalish, M. (1988). Perception of translational heading from optical flow. Journal of Experimental Psychology: Human Perception and Performance, 14, 646–660.
- Wylie, D.W., & Frost, B.J. (1999). Responses of neurons in the nucleus of the basal optic root to translational and rotational flowfields. *Journal of Neurophysiology*, 81, 267–276.

(RECEIVED 8/26/04; REVISION ACCEPTED 5/20/05; FINAL MATERIALS RECEIVED 6/2/05)