

Research Article

VOLUNTARY HEAD MOVEMENT AND ALLOCENTRIC PERCEPTION OF SPACE

Mark Wexler

Collège de France, Paris, France

Abstract—Although visual input is egocentric, at least some visual perceptions and representations are allocentric, that is, independent of the observer's vantage point or motion. Three experiments investigated the visual perception of three-dimensional object motion during voluntary and involuntary motion in human subjects. The results show that the motor command contributes to the objective perception of space: Observers are more likely to apply, consciously and unconsciously, spatial criteria relative to an allocentric frame of reference when they are executing voluntary head movements than while they are undergoing similar involuntary displacements (which lead to a more egocentric bias). Furthermore, details of the motor command are crucial to spatial vision, as allocentric bias decreases or disappears when self-motion and motor command do not match.

An important property of the human visual system is that its viewpoint constantly moves through space, usually as a result of voluntary motor action on the observer's part. At least two reference frames are therefore possible for spatial vision: an egocentric or subjective frame centered on the eye and therefore fixed to the head, and an allocentric or objective, earth-fixed frame.

Perceiving spatial information in an allocentric frame is perhaps the ultimate form of spatial constancy, and has important advantages. An ecological advantage is that it allows an observer to see whether an object is moving at all, rather than moving relative to the observer. An allocentric frame also has computational advantages: The world can be assumed to be stable in this reference frame, and representations of objects and spatial relations do not have to be updated as one moves about. However, retinal data are in an egocentric frame—they contain information only on *relative* motion between object and observer. To convert this to an allocentric frame, *self-motion*—the movement of the eyes through space as the result of eye rotations and head movements—must be evaluated and added to relative motion.

Does spatial vision make use of information about self-motion and, in particular, about head motion? (The rest of this article, which focuses on three-dimensional, or 3-D, vision, concentrates on head movements, which—unlike eye rotations—result in depth information from motion parallax.) One way to address this question is to compare the visual performance of observers in different self-motion conditions, while keeping visual input constant. Held and his colleagues compared actively moving and passively moved human observers, finding effects of voluntary action on visuomotor learning (Held & Freedman, 1963) (and on visual development in cats; Held & Hein, 1963). Though comparisons between actively moving and immobile observers had seemed to show no effect of self-motion on the precision of spatial vision (Rogers & Graham, 1979), it was recently demonstrated that the 3-D shape is perceived differently when observers actively

move about stationary objects than when they remain still while experiencing the same optic flow, generated by object motion (Wexler, Panerai, Lamouret, & Droulez, 2001). The complement to the perception of 3-D shape and motion of objects is the perception of self-motion relative to the environment; it has been shown that extraretinal information about head and eye movements is integrated with optic flow in the perception of heading (Crowell, Banks, Shenoy, & Andersen, 1998; Royden, Banks, & Crowell, 1992).

The use of allocentric reference frames has been studied mainly in the context of spatial memory, where it could constitute a basis for the formation of mental maps that allow for correct spatial behavior, independent of an animal's position or orientation (Tolman, 1948). In the hippocampus of rats, for instance, place cells code position in an allocentric frame (O'Keefe & Nadel, 1978). In monkey hippocampus, researchers have recently found neurons that code allocentric position during active, but not passive, motion (Nishijo, Ono, Eifuku, & Tamura, 1997; but see Hietanen & Perrett, 1996); in monkey posterior parietal cortex, there is a hierarchy of cells that code positions in retinotopic, craniotopic, and spatiotopic (allocentric) frames (Snyder, Grieve, Brotchie, & Andersen, 1998). In human infants, active displacement has been found to favor spatial memory in an allocentric frame (Acredolo, Adams, & Goodwyn, 1984), and a similar result has been obtained in a robotic learning model (Hiraki, Sashima, & Phillips, 1998).

These neurophysiological and behavioral studies indicate that voluntary self-motion plays a role in long-term learning processes in spatial perception and representation. The experiments presented here compared *immediate* visual perception in subjects either engaged in voluntary motion or passively undergoing similar movements. The results show for the first time an immediate effect of voluntary self-motion on spatial vision, and notably on the capacity to use an allocentric reference frame. Two experimental paradigms were used: one in which the choice of reference frame is an explicit and conscious part of the task (Experiment 1), and one in which this choice is unconscious (Experiments 2 and 3).

EXPERIMENT 1

In this experiment, while performing backward-and-forward head movements, subjects viewed a binocularly presented virtual object, also in motion. Their task was to decide whether the object moved, with respect to the otherwise invisible room, in the same direction they did or in the opposite direction—an explicitly allocentric criterion (cf. Wallach, Stanton, & Becker, 1974). As illustrated in Figure 1, the object's movement was yoked to that of the subject with a gain γ : When the subject's head underwent a displacement Δz perpendicular to the image, the object moved by $\gamma\Delta z$ along the same axis. Thus, if the point of subjective equality (where half the answers are "same direction" and half are "opposite direction") falls at $\gamma_0 = 0$, subjects do make use of an allocentric *stationarity* criterion, as instructed; if, however, $\gamma_0 = 1$, an egocentric criterion is used.

Address correspondence to Mark Wexler, LPPA, CNRS/Collège de France, 11, pl. Marcelin Berthelot, 75005 Paris, France; e-mail: wexler@ccr.jussieu.fr.

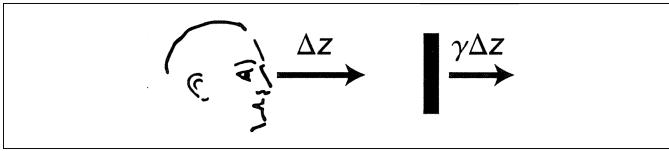


Fig. 1. Schematic conditions of Experiment 1. Subjects engaged in voluntary and involuntary back-and-forth head movements while viewing a virtual object that was projected with binocular disparity. For each displacement Δz of the midpoint between the subject's eyes toward or away from the virtual object, it underwent the same translation (in an earth-fixed, allocentric reference frame) as the subject's head, but with a gain along the z -axis, $\gamma\Delta z$.

The main independent variable of interest was the type of movement: In one block (*voluntary*), the subject performed voluntary backward-and-forward head movements while seated in an immobilized wheelchair; in the other block (*involuntary*), the subject's head was fixed to the back of the wheelchair, which was moved by the experimenter. Trials were automatically aborted and restarted unless trajectories met certain kinematic criteria, so that head trajectories in the two conditions were similar.

Method

Participants

Eleven paid volunteers participated, with 6 performing the voluntary block first, and 5 the involuntary block first.

Apparatus

Head position and orientation were measured with a high-precision head tracker. Stimuli were displayed on a computer monitor coupled to shutter glasses to provide binocular disparity. Except for the stimuli, all experiments were performed in complete darkness. In particular, the monitor frame was invisible. Further details are described in Wexler, Lamouret, and Droulez (2001).

Stimuli

The virtual object projected on the monitor was a 5×5 square grid parallel to the plane of the monitor, with each cell 1 cm in length and edges horizontal and vertical. The initial position of the grid center was (x_0, y_0, Z) , with $Z = -10, 0, \text{ or } 10$ cm, and x_0, y_0 the initial coordinates of the midpoint between the subject's eyes. (In these coordinates, the xy -plane is the monitor with the origin at the center, the x -axis points to the subject's right, the y -axis points upward, and the z -axis points toward the subject.) Between two monitor refreshes, supposing that the subject's head moved by $(\Delta x, \Delta y, \Delta z)$, the grid translated by $(\Delta x, \Delta y, \gamma\Delta z)$, where gain γ varied from -1.1 to $+1.1$ from trial to trial. The grid center thus always remained directly opposite the point between the subject's eyes. The stimulus was viewed binocularly, because without cues to absolute depth, concomitant motion could be interpreted as illusory depth.

Procedure

In the voluntary condition, the subject sat in an immobilized wheelchair; a trial began when the subject's position (midpoint between the eyes) was within 5 cm of the point 100 cm from the monitor

screen, directly opposite its center. The subject performed oscillatory head movement along the z -axis (perpendicular to the monitor). Subjects were instructed to minimize lateral and vertical movement (indeed, the mean RMS displacements in the xy plane did not exceed 28% of those along the z -axis, for any subject in any experiment). The starting direction (forward or backward) was verbally cued. When displacement along the z -axis reached 6 cm, a tone sounded to instruct the subject to change direction; if the displacement exceeded 12 cm, the trial was aborted and started again. The subject performed 2.5 such cycles, with the stimulus grid visible only after the first half-cycle. The subject could then stop moving, and the stimulus was replaced by two icons representing "same direction" and "opposite direction" responses. The subject selected his or her response by pressing a mouse button.

In the involuntary condition, the subject's head was attached to the back of the wheelchair, from which the brakes were removed. The experimenter stood behind the wheelchair and moved it backward and forward (the wheelchair was modified so that it could not turn sideways), with the subject's head motion (as measured by the head tracker) subject to the same kinematic restrictions as in the corresponding voluntary trials.

Results and Discussion

The raw data are shown in Figure 2 as the fraction of "same direction" responses for different values of γ . Individual subjects' data were fitted to the logistic function $1/(1 + 3^{-(\gamma-\gamma_0)/w})$, where the bias γ_0 indicates the point of subjective stationarity, and the width w the precision. Mean biases and widths are shown in Figure 2. The mean point of subjective stationarity was closer to the allocentric criterion ($\gamma_0 = 0$) in the voluntary condition ($\gamma_0 = 0.38$) than in the involuntary condition ($\gamma_0 = 0.57$), and the difference was significant $t(10) = 4.59, p < .001$. The widths, in contrast, were not significantly different in the

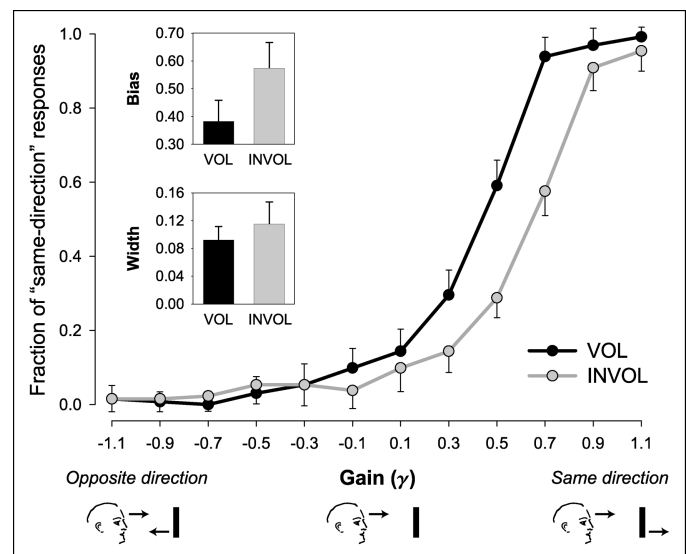


Fig. 2. Results of the voluntary (VOL) and involuntary (INVOL) conditions in Experiment 1. The curves graph responses averaged over subjects, and over all simulated distances (there was no significant effect of distance). Mean bias and width were calculated by fitting individual subjects' data with logistic curves, and averaging the parameters thus obtained. Bars indicate between-subjects standard errors.

Voluntary Motion and Spatial Vision

voluntary and involuntary conditions (0.092 and 0.115, respectively), $r(10) = 1.00$. Learning effects were not confounded with the voluntary/involuntary variable: There was no significant interaction between this variable and the order in which the conditions were presented.

To properly compare performance in the voluntary and involuntary conditions, one has to make sure that head trajectories were very similar in the two conditions, and that any small differences in the trajectories cannot account for the performance differences. This analysis is presented in the appendix.

EXPERIMENT 2

Experiment 1 shows that when using an allocentric criterion is explicitly required, subjects are capable of doing so to a higher degree when actively moving than when passively undergoing similar trajectories. Using an ambiguous stimulus, Experiment 2 investigated whether the same is true when the use of an allocentric frame is an unconscious part of the task.

To resolve ambiguities of movement, the visual system often “attempts,” unconsciously, to minimize motion (Ullman, 1979; Wallach, 1935; Wallach & O’Connell, 1953; Wertheimer, 1912). Recently, my colleagues and I have devised an ambiguous stimulus for the moving observer in which one solution minimizes motion in an allocentric frame, whereas a second solution does so in an egocentric frame (Wexler, Lamouret, & Droulez, 2001). Studying observers in voluntary motion, we found a bias toward the allocentric solution. What happens to this allocentric bias in the case of involuntary motion?

Experiment 2 used the same stimulus (see Fig. 3) as in the second experiment of Wexler, Lamouret, and Droulez (2001). While the subject performed voluntary or involuntary backward-and-forward head movements as in Experiment 1, a set of moving dots was displayed on the computer screen. The dots’ movement was yoked to that of the subject in such a way as to allow the two 3-D interpretations (see Fig. 3b): a plane (*A*) whose center was stationary in an allocentric frame or another plane (*E*) whose center underwent the same movement as the subject, and was therefore stationary in an egocentric frame. The two planes also rotated in the image plane, but about axes that differed by 90° ; the subject’s task, following the presentation of the stimulus, was to indicate its perceived axis of rotation. From this response (which is cognitively opaque), it was possible to determine which solution the subject unconsciously chose—and how the degree of allocentric bias depended on the subject’s motion being voluntary.

Method

Participants

Twelve new subjects participated, with blocked conditions in the order voluntary-involuntary-voluntary.

Apparatus

The apparatus was the same as in Experiment 1, except that the stimulus was presented monocularly.

Stimuli

Stimuli were presented monocularly, and consisted of a set of pixels that were the projections of 50 dots lying on a virtual plane with

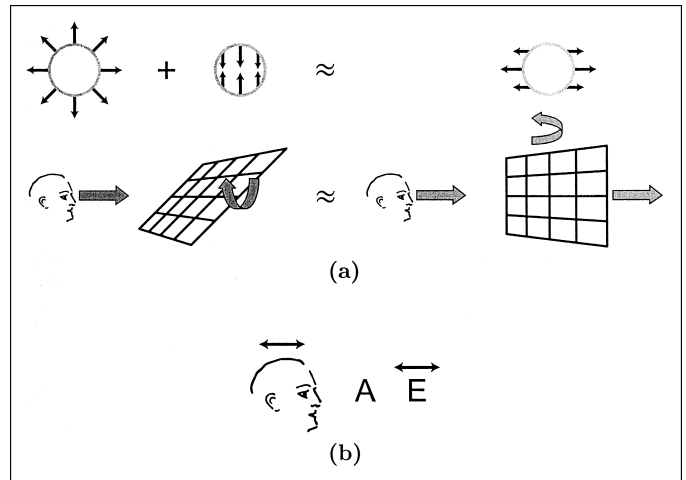


Fig. 3. Illustration of the stimulus used in Experiments 2 and 3, which relied on ambiguity in optic flow. Observers moved toward and away from a set of moving dots and were instructed to indicate the perceived axis of rotation of the plane defined by the dot motion. The stimulus was ambiguous because the optic flow experienced roughly corresponded to two different possibilities, shown in (a): a plane that had a center that was fixed (in an earth-fixed, allocentric frame) and that rotated with a certain speed about an axis perpendicular to its normal (left) and a plane that had a center that was fixed with respect to the moving subject (i.e., that reproduced the subject’s translatory movements) and that rotated at the same speed as the first plane, but whose orientation and axis of rotation were shifted by 90° with respect to those of the first plane. Thus, the moving observers could perceive a three-dimensional configuration that either minimized motion in an allocentric frame, *A*, or minimized motion in an egocentric frame, *E* (b). For further details, including a mathematical derivation, see Wexler, Lamouret, and Droulez (2001), as well as <http://wexler.free.fr/voluntary.shtml>.

slant σ of 45° and tilt chosen from the set $0^\circ, 30^\circ, \dots, 330^\circ$. On average, the size of the stimulus was 10° . The density of the dots was circularly symmetric (to minimize texture depth cues), and proportional to $r^{-4/3}$, with r the distance from the center: Lower density at the edges made them irregular and less salient. The virtual object rotated about a frontal axis perpendicular to its normal, with angular speed $v/\tan \sigma$, where v was the subject’s speed along the z -axis normalized by the distance from the stimulus—so that the two maxima of rigidity were the *A* and *E* solutions described earlier (Wexler, Lamouret, & Droulez, 2001).

Procedure

The procedure was like that of Experiment 1, with minor changes (1.5 cycles of motion, starting distance of 90 ± 10 cm, amplitude of 7 cm, and a limitation of the period of oscillation to below 6 s). During the response phase, a probe line could be rotated by inclining a joystick. Subjects adjusted the probe so that it appeared to coincide with the rotation axis of the stimulus (or its projection).

Results and Discussion

The distributions of axis-angle responses, with respect to the axis of the *A* solution, are shown in Figure 4. There is a clear difference between the conditions: Subjects chose the *A* solution more often in the

voluntary than in the involuntary condition. For quantifying this difference, the *allocentricity* is defined as the fraction of trials in which responses were closer to the *A* than to the *E* solution. Allocentricity, also shown in Figure 4, was significantly higher in the voluntary condition (.543) than in the involuntary condition (.257), $t(11) = 6.8$, $p < 10^{-4}$. This difference was not due to any learning or sequence effects: *t* tests showed no significant difference in allocentricity between the first and second voluntary blocks. As shown in the appendix, trajectories in the voluntary and involuntary conditions were very similar, and the small differences do not account for the differences in perfor-

mance. These results show that when spatial-reference-frame criteria are unconscious, rather than explicit, as in Experiment 1, subjects also make use of an allocentric reference frame more during voluntary than involuntary motion.

EXPERIMENT 3

The results of Experiment 2 do not tell us whether *any* voluntary action resulting in the movement of the eye through space is sufficient to trigger a bias toward an allocentric least-motion criterion (the *trig-*

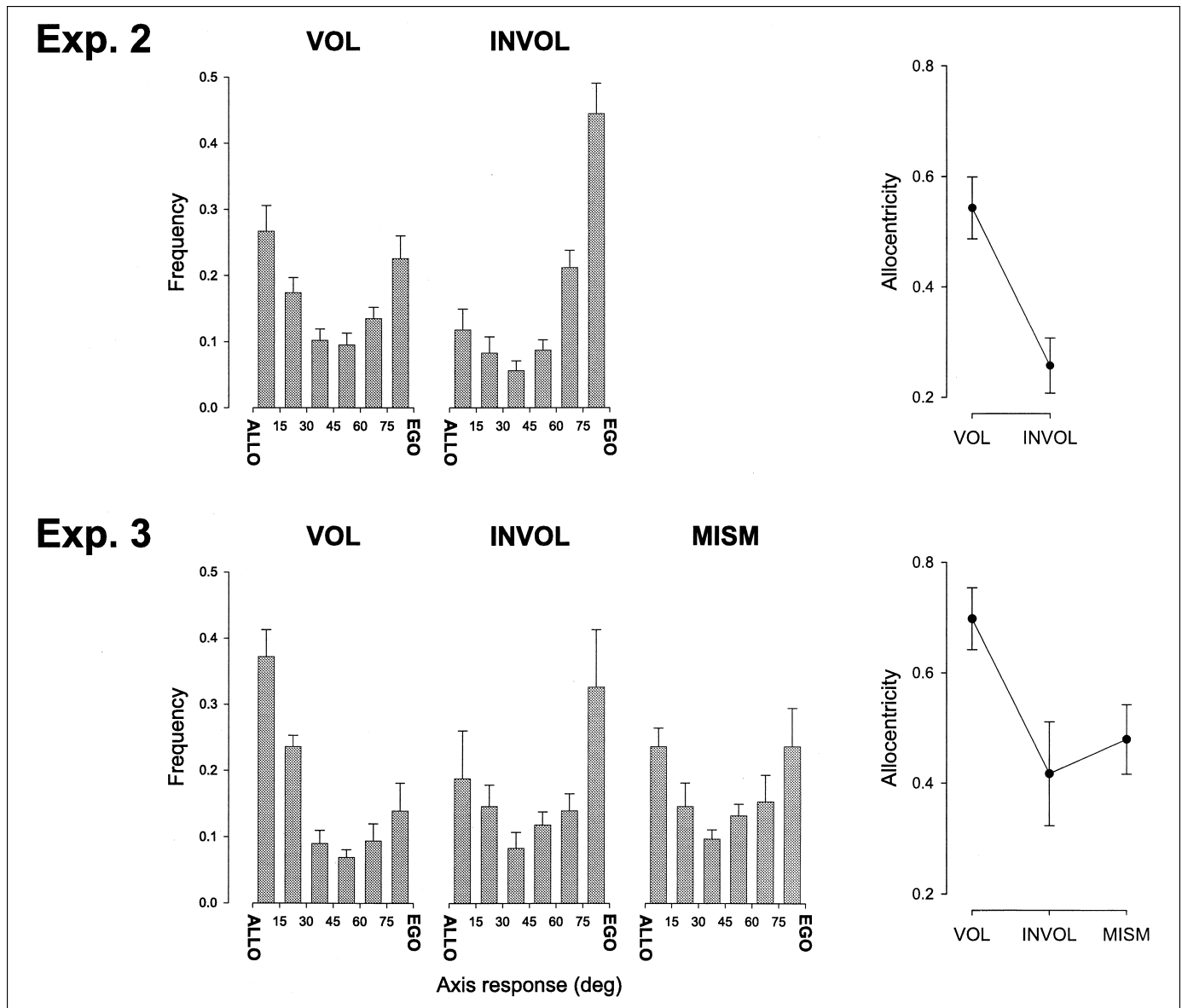


Fig. 4. Results of Experiments 2 (top) and 3 (bottom). “ALLO” and “EGO” represent the limits of the allocentrically and egocentrically most stationary solutions, respectively. The histograms show distributions of the absolute difference between the axis angle of responses and the axis angle of the allocentrically most stationary solution. The curves show the allocentricity measure, the fraction of responses closer to the solution that minimizes motion in an allocentric reference frame than to the solution that minimizes motion in an egocentric reference frame. Bars represent between-subjects standard errors. VOL = voluntary condition; INVOL = involuntary condition; MISM = mismatch condition.

Voluntary Motion and Spatial Vision

ger hypothesis) or whether, in the active observer, the details of the motor command lead to a predicted self-motion, which is used to compensate egocentric sensory data and to convert it to an allocentric frame (the *prediction hypothesis*). Experiment 3 distinguished between these hypotheses by adding a *mismatch* condition to the design of Experiment 2. In the mismatch condition, observers actively generated self-motion by turning the wheels of a wheelchair with their arms. Because none of the observers had had any experience with this type of locomotion, resulting self-motion did not match the details of the motor command. The trigger hypothesis predicted that the results in the mismatch condition would resemble those in the voluntary condition, but according to the prediction hypothesis, results in the mismatch condition would resemble those in the involuntary condition.

Method

The method was identical to that of Experiment 2, except for the additional mismatch condition, in which the subject's head was attached as in the involuntary condition, but the motion was driven by the subject's turning the wheelchair wheels with his or her arms. Six new subjects participated (none with prior experience of arm-driven locomotion in a wheelchair, and none needing more than a few minutes to learn to operate the wheelchair with the required kinematics). Half performed the conditions in the order voluntary-involuntary-mismatch-voluntary, and half performed them in the order voluntary-mismatch-involuntary-voluntary.

Results and Discussion

Results are shown in Figure 4. As in Experiment 2, subjects had a significantly higher allocentricity in the voluntary than in the involuntary condition, $t(5) = 4.97, p < .01$. (The subjects in Experiment 3 had higher mean allocentricity than those in Experiment 2, but these between-group differences were not significant. The voluntary-involuntary differences were very similar in the two groups: .286 in Experiment 2, .281 in Experiment 3.) Subjects had a significantly higher allocentricity in the voluntary than in the mismatch condition, $t(5) = 3.61, p < .05$, whereas there was no significant difference between the involuntary and mismatch conditions, $t(5) = 1.12, p = .3$. Thus, although it is impossible to exclude the contribution of voluntary arm motion in the mismatch condition, it is insufficient to account for the degree of allocentric bias during voluntary motion. These results therefore agree with the prediction hypothesis, and contradict the trigger hypothesis. Thus, in voluntary motion, the detailed motor command is converted into a metric prediction of self-motion (unless there is a mismatch), which is then used to convert visual data to an allocentric frame.

GENERAL DISCUSSION

The results of three experiments show, for the first time, that voluntary motion can play an important role in the immediate visual perception of 3-D object motion and shape, and notably in the use of allocentric spatial criteria. Experiment 1 shows that when the task involves conscious allocentric criteria (i.e., the explicit judgment of motion in an allocentric frame), subjects are better able to apply such criteria when actively generating their head movements than when passively undergoing similar trajectories. Experiment 2 shows that a similar result

holds in a case in which allocentric criteria are unconscious: In unconsciously applying least-motion criteria to determine 3D motion and structure from 2D optic flow, subjects are more likely to apply such criteria relative to an allocentric reference frame while undergoing voluntary motion than when experiencing passive motion. Finally, Experiment 3 shows that in the case of voluntary motion, the details of the motor command play an important role: A mismatched motor command leads to performance that is similar to performance when motion is involuntary.

Extraretinal self-motion information can be categorized into two types, *motor* and *proprioceptive*. Motor information arises from the origin of the motor signal in the brain; the reafferent copy or corollary discharge of the motor signal is used in vision (Sperry, 1950; von Holst & Mittelstaedt, 1950). Proprioceptive information arises from sensory feedback once the subject is moving, in particular, from vestibular and somatosensory signals. The main difference between voluntary and involuntary motion is that although proprioceptive signals are available in both types of motion, motor signals are absent or highly diminished in involuntary motion. However, in the present experiments, some secondary somatosensory signals also differed between voluntary and involuntary conditions; in general, vestibular signals may be different in the case of voluntary and involuntary head motion (McCrea, Gdowski, Boyle, & Belton, 1999; Roy & Cullen, 2001). However, if the robust differences between voluntary and involuntary motion demonstrated here are due to motor signals, one can conclude that motor signals in head motion play an important role in the allocentric perception of space. Furthermore, from the results of Experiment 3, we can conclude that it is not the mere presence of a corollary discharge, but the details of the motor command that are crucial to spatial vision. Insofar as vision in an allocentric frame is a form—perhaps the ultimate form—of spatial constancy, this finding echoes the role of efference copy in spatial constancy in the context of eye movements (Duhamel, Colby, & Goldberg, 1992; Guthrie, Porter, & Sparks, 1983; Stark & Bridgeman, 1983; Sommer & Wurtz, 2002; Stevens et al., 1976).

What role could learning play in the incorporation of self-motion signals in spatial vision? For instance, would the results of the mismatch condition be different in wheelchair-bound subjects used to this form of locomotion? Could subjects learn to make do with nothing but proprioception if they have sufficient exposure to passive locomotion? The last proposition seems doubtful, given the existing prevalence of passive motion (e.g., in automobiles) in our culture. Held and Freeman (1963) found that visuomotor learning took place in both voluntary and involuntary locomotion, but proceeded faster in the voluntary case. It would be useful to examine how the effects found in the present study evolve with learning.

The experiments presented here provide psychophysical evidence that human spatial vision uses an allocentric reference frame more often in voluntary self-motion and an egocentric frame more often in involuntary motion, that this is so whether the reference frame is a conscious or unconscious part of the subject's task, and that the voluntary-involuntary difference diminishes or disappears if there is not a detailed match between the motor command and the observer's displacement. These results show not only that the observer's self-motion cannot be disregarded in spatial vision, but also that the observer's active role in initiating and producing that motion is crucial.

Acknowledgments—This work was partly supported by the CNRS and by a grant from Essilor International. I thank Ivan Lamouret, Jeroen van Boxtel, and Jacques Droulez for discussions.

REFERENCES

- Acredolo, L.P., Adams, A., & Goodwyn, S.W. (1984). The role of self-produced movement and visual tracking in infant spatial orientation. *Journal of Experimental Child Psychology*, *38*, 312–327.
- Crowell, J.A., Banks, M.S., Shenoy, K.V., & Andersen, R.A. (1998). Visual self-motion perception during head turns. *Nature Neuroscience*, *1*, 732–737.
- Duhamel, J.R., Colby, C.L., & Goldberg, M.E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, *255*, 90–92.
- Guthrie, B.L., Porter, J.D., & Sparks, D.L. (1983). Corollary discharge provides accurate eye position information to the oculomotor system. *Science*, *221*, 1193–1195.
- Held, R., & Freedman, D.J. (1963). Plasticity in human sensorimotor control. *Science*, *142*, 455–462.
- Held, R., & Hein, A. (1963). Movement-produced stimulation in the development of visually guided behavior. *Journal of Comparative and Physiological Psychology*, *56*, 872–876.
- Hietanen, J.K., & Perrett, D.I. (1996). A comparison of visual responses to object- and ego-motion in the macaque superior temporal polysensory area. *Experimental Brain Research*, *108*, 341–345.
- Hiraki, K., Sashima, A., & Phillips, S. (1998). From egocentric to allocentric spatial behaviour: A computational model of spatial development. *Adaptive Behavior*, *6*, 371–391.
- McCrea, R.A., Gdowski, G.T., Boyle, R., & Belton, T. (1999). Firing behavior of vestibular neurons during active and passive head movements: Vestibulo-spinal and other non-eye-movement related neurons. *Journal of Neurophysiology*, *82*, 416–428.
- Nishijo, H., Ono, T., Eifuku, S., & Tamura, R. (1997). The relationship between monkey hippocampus place-related neural activity & action in space. *Neuroscience Letters*, *226*, 57–60.
- O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford, England: Oxford University Press.
- Rogers, B., & Graham, M. (1979). Motion parallax as an independent cue for depth perception. *Perception*, *8*, 125–134.
- Roy, J.E., & Cullen, K.E. (2001). Selective processing of vestibular reafference during self-generated head motion. *Journal of Neuroscience*, *21*, 2131–2142.
- Royden, C.S., Banks, M.S., & Crowell, J.A. (1992). The perception of heading during eye movements. *Nature*, *360*, 583–585.
- Snyder, L.H., Grieve, K.L., Brotchie, P., & Andersen, R.A. (1998). Separate body- and world-referenced representations of visual space in parietal cortex. *Nature*, *394*, 887–891.
- Sommer, M.A., & Wurtz, R.H. (2002). A pathway in primate brain for internal monitoring of movements. *Science*, *296*, 1480–1482.
- Sperry, R.W. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *Journal of Comparative and Physiological Psychology*, *43*, 482–489.
- Stark, L., & Bridgeman, B. (1983). Role of corollary discharge in space constancy. *Perception & Psychophysics*, *34*, 371–380.
- Stevens, J.K., Emerson, R.C., Gerstein, G.L., Kallos, T., Neufeld, G.R., Nichols, C.W., & Rosenquist, A.C. (1976). Paralysis of the awake human: Visual perceptions. *Vision Research*, *16*, 93–98.
- Tolman, E.C. (1948). Cognitive maps in rats and man. *Psychological Review*, *55*, 189–208.
- Ullman, S. (1979). *The interpretation of visual motion*. Cambridge, MA: MIT Press.
- von Holst, E., & Mittelstaedt, H. (1950). Das reafferenzprinzip. *Naturwissenschaften*, *37*, 464–476.
- Wallach, H. (1935). Über visuell wahrgenommene Bewegungsrichtung. *Psychologische Forschung*, *20*, 325–380.
- Wallach, H., & O'Connell, D.N. (1953). The kinetic depth effect. *Journal of Experimental Psychology*, *45*, 205–217.
- Wallach, H., Stanton, L., & Becker, D. (1974). The compensation for movement-produced changes in object orientation. *Perception & Psychophysics*, *15*, 339–343.
- Wertheimer, M. (1912). Experimentelle Studien über das Sehen von Bewegung. *Zeitschrift für Psychologie*, *61*, 161–265.
- Wexler, M., Lamouret, I., & Droulez, J. (2001). The stationarity hypothesis: An allocentric criterion in visual perception. *Vision Research*, *41*, 3023–3037.
- Wexler, M., Panerai, F., Lamouret, I., & Droulez, J. (2001). Self-motion and the perception of stationary objects. *Nature*, *409*, 85–88.

(RECEIVED 5/7/02; REVISION ACCEPTED 10/19/02)

APPENDIX

In comparing the visual perception performance across movement conditions in all three experiments, a crucial question is, to what extent are any movement trajectory differences responsible for the effects observed? By *trajectories*, I mean the translations of the eye (or eyes) during the portion of each trial in which the stimulus was visible. The crucial z -components of the trajectories are shown in Figure A1, which qualitatively demonstrates that trajectories were very similar across conditions in each experiment. Three types of quantitative analyses are summarized here. For all three experiments, these analyses showed that (a) the trajectory differences were minor, and (b) such

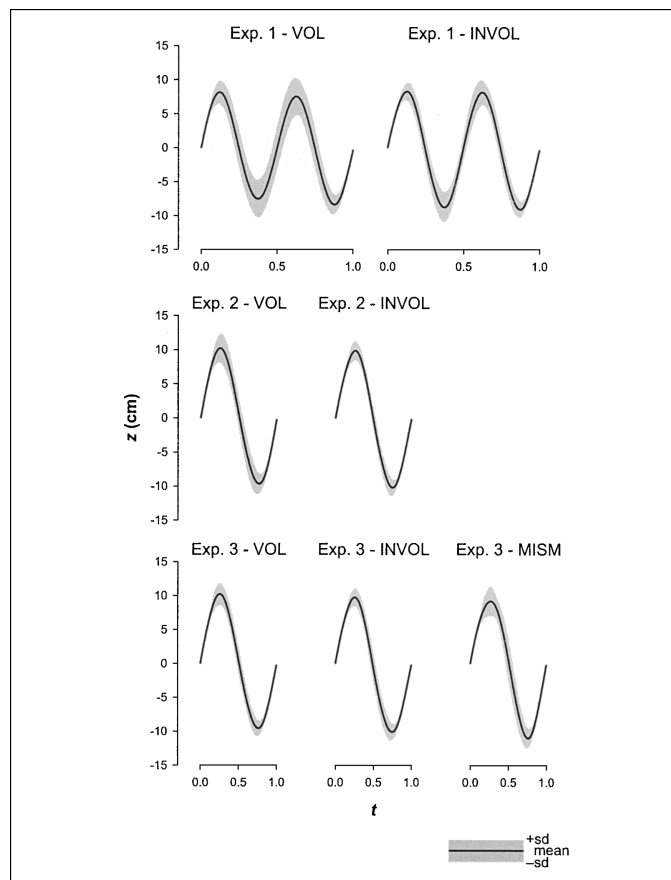


Fig. A1. Average eye displacements along the z -axis, normalized by trial duration, for all subjects in all conditions of all three experiments, during the portion of each trial for which the stimulus was visible (2 cycles in Experiment 1, 1 cycle in Experiments 2 and 3). Gray shading represents standard deviation. VOL = voluntary condition; INVOL = involuntary condition; MISM = mismatch condition.

trajectory differences as existed between the conditions cannot account for the effects observed.

Trajectory Variations

One way of defining the difference between trajectories in two conditions is to compare variations between conditions with those within conditions. To define a measure inverse to variation, I used the mean correlation between z -displacements in all pairs of trials; to calculate correlations between unequal-length trials, the z -coordinate was resampled in 100 time bins in each trial. For example, in Experiment 1, the mean within-condition correlation was .867 in the voluntary condition and .935 in the involuntary condition; the mean correlation between these two conditions was .894. This means that although trajectory variations were lowest in the involuntary condition (which is understandable, because the same experimenter always produced those trajectories), the differences between trajectories in the two conditions were lower than the variations within the voluntary condition, and approximately equal to average variations within the two conditions. Similar results hold for Experiments 2 and 3.

Homogenized Trajectories

To test whether the small differences in trajectory kinematics could be responsible for the performance differences between the conditions, I subdivided trials

Voluntary Motion and Spatial Vision

into narrow, homogeneous subsets by various kinematics parameters. In Experiment 1, for example, the RMS z -speed of 87% of trials in the voluntary and involuntary conditions fell between 15 and 28 cm/s. These trials were divided into 13 equal bins, each bin 1 cm/s wide and each having a nearly uniform speed distribution. Within every bin, bias was lower (closer to zero) in the voluntary condition than in the involuntary condition: A nonparametric test for difference in bias between the two conditions would therefore yield a p below .05. A similar analysis for z -displacements yielded a similar result, and so did corresponding analyses for allocentricities in Experiments 2 and 3. Thus, when analyses compare across conditions only those subsets of trials in which the distributions of a given kinematic parameter are nearly identical, the effects are the same as when all trials are included. Therefore, any variations in kinematic parameters are unlikely to be responsible for the differences in visual performance between conditions.

No Correlations Between Trajectories and Performance

Finally, as an additional analysis to test for any dependence of responses on trajectory kinematics, the following quantities were regressed against the axis-angle responses in Experiments 2 and 3, within each block for each subject: trial duration, RMS of z -displacements, RMS of xy -displacements, RMS of z -speeds, and RMS of z -accelerations. In t tests on Fisher-transformed correlation coefficients over all subjects for each quantity in each block, none of the kinematic quantities was found to have any significant effect on responses, in any condition. Thus, despite the small differences between trajectory kinematics in the voluntary and involuntary conditions, it is reasonable to compare responses in these conditions, because the responses did not depend in any significant or consistent way on the kinematics.