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Visual self-motion perception during head turns

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Extra-retinal information is critical in the interpretation of visual input during self-motion. Turning our eyes and head to track objects displaces the retinal image but does not affect our ability to navigate because we use extra-retinal information to compensate for these displacements. We showed observers animated displays depicting their forward motion through a scene. They perceived the simulated self-motion accurately while smoothly shifting the gaze by turning the head, but not when the same gaze shift was simulated in the display; this indicates that the visual system also uses extra-retinal information during head turns. Additional experiments compared self-motion judgments during active and passive head turns, passive rotations of the body and rotations of the body with head fixed in space. We found that accurate perception during active head turns is mediated by contributions from three extra-retinal cues: vestibular canal stimulation, neck proprioception and an efference copy of the motor command to turn the head.

As we move through the environment, the projected positions of objects in the image formed on the retina change in predictable ways. For example, if we walk or drive in a straight line, our self-motion produces a radial pattern of motion in the retinal image (**Fig. 1a**). The direction toward the center or focus of the radial expansion corresponds to our direction of motion[1]. Recreating this pattern of retinal-image motion by viewing a film or computer display depicting our forward motion can cause a compelling sensation that we are in fact moving forward[2], and under a variety of conditions we can accurately estimate where we are going in the simulated scene[3,4].

When we smoothly shift gaze direction by turning the eyes or head (for example, to look at a moving object or at a stationary object to the side) while still moving in a straight line, the pattern of retinal-image motion is more complex (**Fig. 1b**). We can recreate this type of retinal motion pattern by having observers hold the eye still while monocularly viewing a display that simulates both their forward motion and an eye movement. In this case, observers report that they are moving along a curved trajectory (as though turning a car while looking forward through the windshield) rather than along the depicted linear path. When they are asked to adjust the position of a marker at a certain simulated distance in front of them—iteratively, by making a 'left' or 'right' response after viewing each of a series of simulations—until it appears to sit upon their future path (such that they would hit it if the simulation continued), their responses are strongly biased in the direction of the perceived path curvature (rightward in **Fig. 1b**)[5–8]. On the other hand, this type of self-motion judgment is quite accurate when the identical pattern of retinal image motion is created by having observers view a display like that in Fig. 1a while turning the eye to pursue a target that moves across it[5,6,8,9]. Observers typically report that they appear to be moving on a straight rather than a curved path.

The only difference between this case and the preceding one is extra-retinal information that the observer's visual system has about the eye movement. This information mainly consists of a signal from a part of the brain involved in the control of eye movements describing the motor command to turn the eye, commonly referred to as an efference copy[2]. The visual system uses this information to compensate for the effects of the eye movement on the retinal motion pattern; previous research using self-motion judgments indicates that this compensation is nearly complete[5,6,8,9].

In everyday life, smooth gaze shifts tend to involve the head as well as the eyes[10]; however, little is known about visual compensation for smooth gaze shifts produced by turning the head. The effect on the retinal image is roughly the same whether the gaze is shifted by eye or head movement. The case of head movements is more complex and potentially very interesting because there are three extra-retinal cues that could allow us to compensate for the effects of head turns on the retinal image. When the head turns in space, the vestibular semicircular canals in the inner ear are stimulated; over a broad range of rotation rates, they provide a signal that is proportional to the head's angular velocity[2]. When the head turns with respect to the body, proprioceptive sensors in the neck are stimulated and provide information about the neck's orientation on the body[2]. ('Proprioception' is the ability to feel the positions of one's body parts.) Finally, when we actively turn our heads, an efference copy of the motor command to turn the head may be sent to the visual system.

The experiments reported here answer two questions: first, do we perceive self-motion as accurately during head turns as during eye movements, and second, which of the three extra-retinal cues present during head turns—vestibular canal stimulation, neck proprioception and efference copy—are involved in this behavior, and how do they interact? We found that self-motion judgments are as accurate during head turns as during
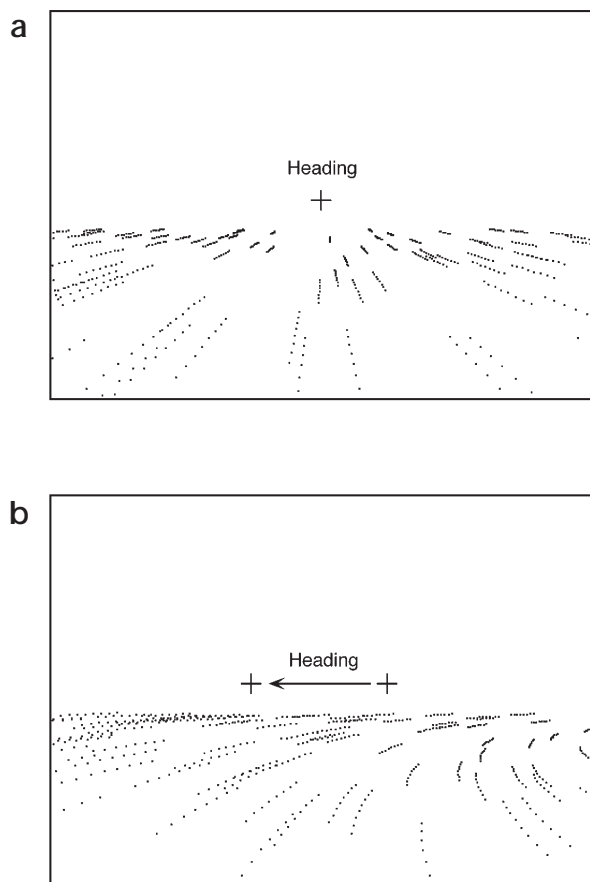
Fig. 1. Retinal-image motions created by forward observer motion. These diagrams represent the trajectories of dots in displays created by simulating (**a**) linear forward self-motion across a ground plane and (**b**) the same linear self-motion combined with a simulated rightward constant-velocity gaze rotation (for example, a rightward eye or head movement). In (a), all dot motions are directed away from the point the observer is moving toward (the '+'), and self-motion judgments are accurate. The pattern in (b) is generally misinterpreted by observers as simulating self-motion on a path that curves to the right with the direction of gaze always forward (as though driving a car around a bend), leading to large errors in perceived self-motion. The visual information that would allow the brain to correctly interpret this motion pattern is subtle. The direction of self-motion or heading is constant with respect to the simulated world, whereas the simulated gaze direction rotates to the right; this means that the instantaneous heading moves to the left across the display over time, as shown by the arrow. Objects in the foreground (at the bottom of the display) tend to move radially away from the heading, so their trajectories will curve to the right as the heading drifts leftward. If, on the other hand, the gaze rotation were created by driving around a bend in the road, the heading would remain fixed on the screen (in the reference frame of a vehicle going around a curve, the instantaneous direction of translation is always straight ahead), resulting in slightly less curved trajectories on the screen.

eye movements. No single extra-retinal cue is sufficient to guarantee accurate perception of self-motion, and some observers require that all three cues be consistent.

Results

To quantify how effective different extra-retinal cues are in mediating accurate self-motion judgments, we compared conditions in which specific extra-retinal cues were available to a condition in which they were not. The 'simulated pursuit' condition, in which the observer held the gaze fixed while the display simulated a gaze shift, contained no extra-retinal cues. The sequence of retinal images in this condition is identical to that in all of the real pursuit conditions; thus any differences in performance reflect the compensating effects of extra-retinal cues. Judgments in this condition were biased by an amount that increased in proportion to the simulated gaze rotation rate (**Fig. 2**); at a simulated rate of 9° per second, errors on the order of 20° were common. These steep functions are the benchmark for performance in the absence of extra-retinal compensation; the best-fitting lines to these data are re-plotted in each panel of Fig. 3 to simplify comparisons. At the other extreme, perfect performance or complete compen-

sation (small errors at all rotation rates) would be represented by a horizontal line at or near a path error of 0°. The effectiveness of a given extra-retinal cue is indicated by how much it decreases the slope of the error function relative to that in the simulated-pursuit condition; more effective cues yield shallower slopes.

We found that compensation for gaze shifts does occur during head turns (**Fig. 3b**). During 'active head pursuit', in which observers pursued a moving target by turning the head with the eye fixed in the orbit, judgments were very accurate and comparable to judgments during 'eye pursuit' (**Fig. 3a**), in which the eye turned in the orbit to track the target with the head stationary. The slopes of the symbol sets in these graphs are roughly zero, indicating almost complete compensation for both types of gaze shift. Perception of self-motion is accurate during active head turns.
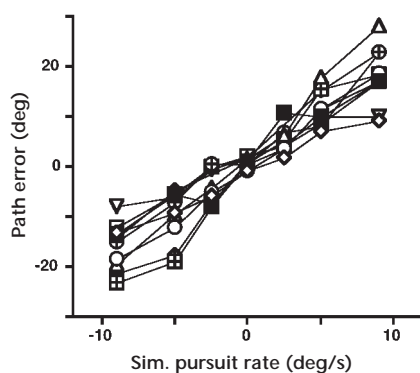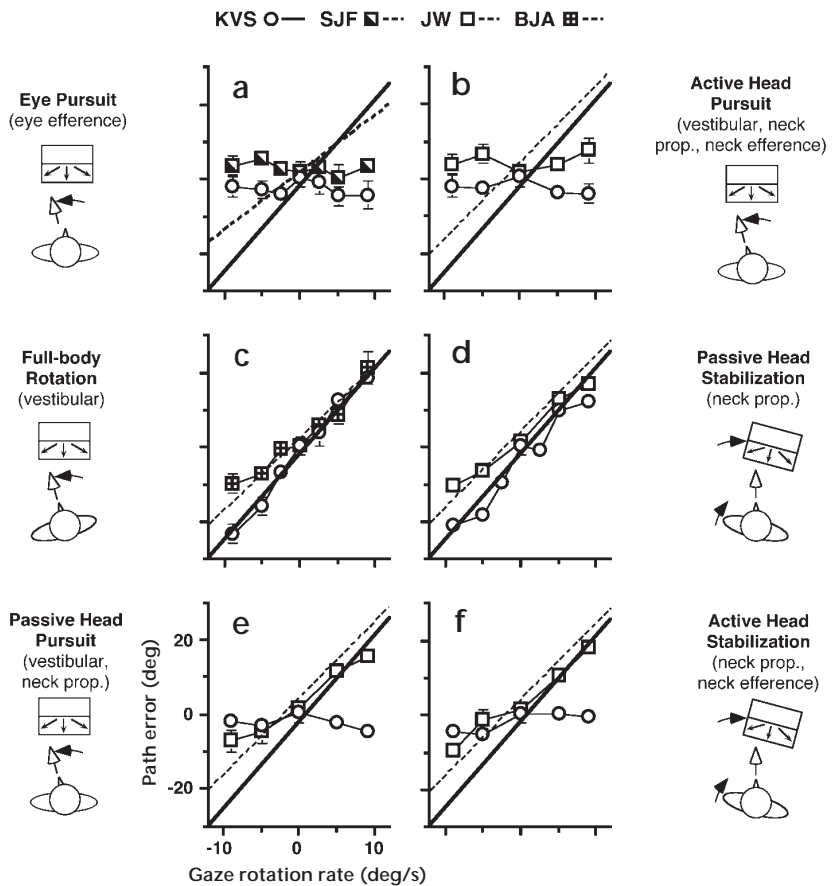

Fig. 2. Data for ten observers in the simulated pursuit condition. Each symbol type represents a different observer. Path error (see Methods) increases in proportion to the simulated pursuit rate, though the proportionality constant or slope varies from one observer to the next. Retinal image sequences are identical to the various real pursuit conditions, but there are no extra-retinal cues indicating that the gaze is shifting. These data are the baseline against which performance in all subsequent conditions is measured; we quantify extra-retinal gaze-shift compensation by the extent to which a given extra-retinal cue or cues improves performance (that is, reduces the slope of the function of path error versus pursuit rate) over this condition.

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Fig. 3. Real pursuit conditions and data from typical observers. Path errors are plotted as a function of gaze rotation rate. Symbols represent data for the conditions described; thick lines were fit to the data from the simulated pursuit condition (**Fig. 2**). Error bars represent standard deviations of the staircase reversal values. **(a, b)** The full-cue conditions: eye pursuit and active head pursuit. Self-motion path judgments were accurate and independent of pursuit rate in both conditions. Some observers found constant-rate head turns difficult to perform, resulting in increased variability. **(c, d)** The single-cue conditions: full-body rotation and passive head stabilization. Self-motion path judgments were erroneous; symbols lie on top of the corresponding lines from the simulated-pursuit condition. **(e, f)** The two-cue conditions: passive head pursuit and active head stabilization. Accuracy varied considerably in these conditions. One of the representative observers (KVS) performed well in both conditions, whereas the other (JW) performed well in neither. Other observers performed well in one condition but not the other.

KVS ○— SJF ◼-⋅⋅ JW ☐-⋅⋅ BJA ⊞-⋅⋅

Eye Pursuit (eye efference)

Active Head Pursuit (vestibular, neck prop., neck efference)

Full-body Rotation (vestibular)

Passive Head Stabilization (neck prop.)

Passive Head Pursuit (vestibular, neck prop.)

Active Head Stabilization (neck prop., neck efference)

Path error (deg)

Gaze rotation rate (deg/s)

During active head turns, all three extra-retinal cues—vestibular canal stimulation, neck proprioception and neck efference copy—indicate that the head is turning. To determine which cues are more important, we presented observers with situations in which only one cue or a pair of cues was consistent with a head turn. Not all combinations of these cues are realizable, even under experimental conditions.

The next pair of experiments isolated single cues. During 'full-body rotation', the observer's entire body was rotated by a motor-ized chair while the head was held fixed with respect to the body by a chinrest attached to the chair. In this situation, only the vestibular canal stimulation was consistent with a head turn. During 'passive head stabilization', on the other hand, the body rotated while the head was held fixed in space by a chinrest attached to the ceiling. In this condition, the head rotated with respect to the body, but not with respect to space, so only neck proprioception was consistent with a head turn. Neither of these conditions yielded accurate performance (**Fig. 3c** and **d**); the

Fig. 4. Are observers really passive during passive head pursuit? **(a)** Measurements of the forces between the observer's head and the apparatus during passive head pursuit (gray lines show the mean force ± one standard deviation in Newtons at each instant in time across all the trials of a run) and a control condition ('at rest', solid black circles) in which the observer's head was moved to a given angle and he relaxed as much as possible during the measurement.

(b) The same force measurements grouped into trials in which the observer indicated he would pass to the left of the response marker (black lines) or to its right (gray lines). The only visible separation between the means (around 0°) is in the opposite direction to the head movement. The dotted black line represents a trial in which the observer actively turned his head to pursue the target while the apparatus was turned by motor as before; the self-motion percept was similar to that in a preceding passive trial.
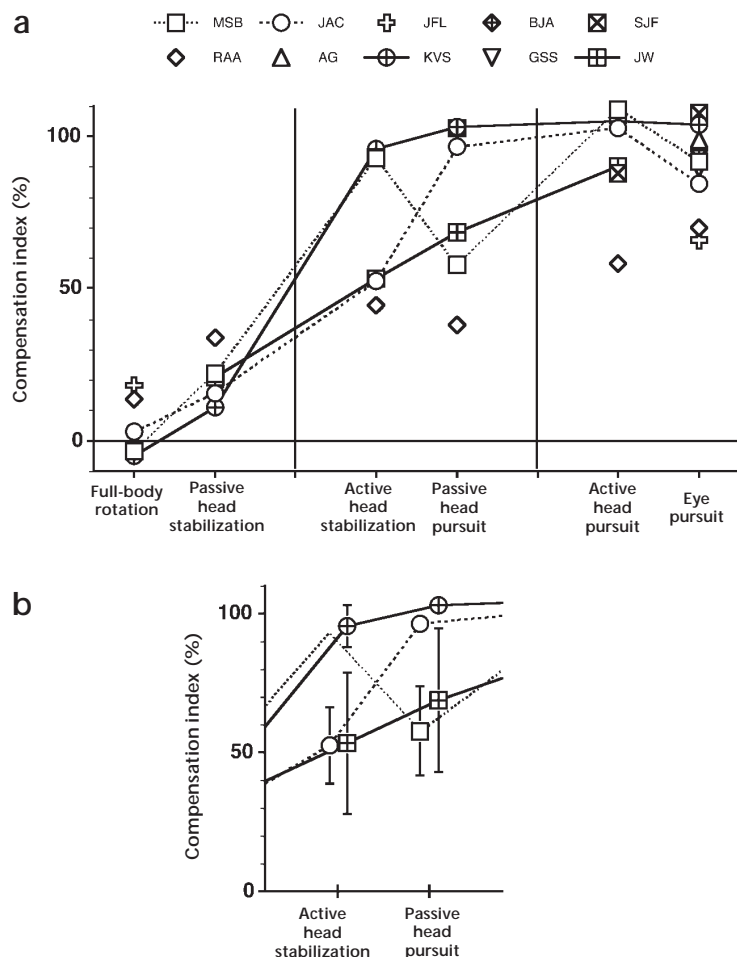
a

b
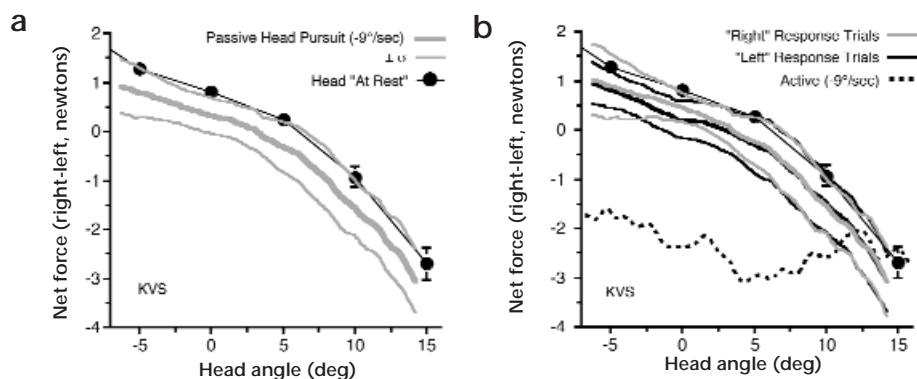
Fig. 5. Summary of results. **(a)** Performance comparison for all observers but one (see text) across all conditions. For each observer in each condition (many observers did not run in all conditions), we plot the compensation index, defined to be CI = $100*(1 - M/M_{sim})$, where M_{sim} is the slope of that observer's error function in the simulated-pursuit condition and M is that observer's slope in the condition in question. A value of 0% indicates that the errors are as large as in the simulated condition, whereas 100% indicates a slope of zero, or perfect compensation. Compensation is consistently high in the full-cue conditions (eye and active head pursuit) and low in the single-cue conditions (full-body rotation and passive head stabilization). In the two-cue conditions (active head stabilization and passive head pursuit), we found different patterns of behavior, as shown by the lines connecting four of the observers' symbols. **(b)** Because of the inter-observer differences in the active head stabilization and passive head pursuit conditions, we ran 3–5 replications for 4 observers in these conditions. Error bars indicate the standard deviations of the observed compensation indices; for KVS and JAC in the passive head pursuit condition, they were smaller than the symbols, at 2.4% and 2.6%, respectively. We do not have replicates for MSB in active head stabilization.

symbols lie on top of or close to the solid lines representing simulated pursuit. Single extra-retinal cues did not help much in compensating for the effects of gaze shifts.

The possibility remained that judgments are only accurate during active movements, implying that efferent signals are the determining factor. It would be extremely difficult to isolate a neck efference copy without accompanying muscle sensations; thus, the remaining two experiments examined the effectiveness of manipulations of efference copy in combination with other cues. In 'passive head pursuit', we removed the efference copy cue normally available during an active head turn by using a motorized chin/head rest to turn the head. In 'active head stabilization', we combined efference copy with neck proprioception; the body was turned while the observer actively counter-rotated the head to hold it fixed in space. If efference copy is the single important cue, judgments should be accurate in the latter experiment, but not the former. It should be noted, however, that the amount of effort required is less during active head stabilization than during normal active head pursuit because the observer does not have to overcome the head's inertia. We observed a variety of behavior patterns in these two experiments (**Fig. 3e** and **f**). For example, one of the two observers depicted (KVS) performed very well in both conditions, whereas the other (JW) demonstrated moderate performance in both. Neither pattern is consistent with the use of neck efference copy alone: poor performance during active head stabilization indicates that efference copy is insufficient for com-

plete compensation (with the caveat regarding the smaller effort required in this condition); accurate performance during passive head pursuit implies that efference copy is not necessary.

We ran a control experiment to ensure that the two observers who performed well during passive head pursuit (KVS and JAC) were not actively assisting the head turn instead of being truly passive as instructed. In this experiment, force transducers were mounted between the observer's head and the apparatus. Although there was a small difference in force between passive head pursuit and a baseline 'at rest' condition for observer KVS (**Fig. 4a**), the magnitude of this difference was uncorrelated with the observer's response (**Fig. 4b**). In other words, a greater, but still small, force in the direction of the head turn did not enhance gaze-shift compensation. Actively turning the head while the motor turned the apparatus resulted in considerably greater forces (dashed curve) but did not change the observer's self-motion percept. The other observer's data were similar. We take these results to indicate that the greater degree of compensation exhibited by these observers during passive head pursuit was probably not due to active assistance.

We used the slopes of each observer's data (with one exception, an observer who showed no compensation under any conditions) in each condition to calculate a 'compensation index'; this index quantifies the effectiveness of a given extra-retinal cue or combination of cues in mediating accurate self-motion judgments (**Fig. 5a**). The index is 0% when the slope is as large, as in

simulated pursuit; it is 100% when the slope is zero, indicating perfect compensation. In the two full-cue conditions, active head pursuit and eye pursuit, most observers judged self-motion accurately; mean compensation was 90% during eye pursuit and 94% during active head pursuit. In the single-cue conditions, full-body rotation and passive head stabilization, performance was consistently poor, 4% and 21%, respectively. In the two-cue conditions, active head stabilization and passive head pursuit, we found different patterns of behavior, as shown by the lines connecting four of the observers' symbols. Average compensation in these cases was 68% and 78%, respectively.

To determine whether these apparently different patterns of behavior are stable, we ran a number of replications (3–5 for each of 4 observers) in these two conditions; no two runs were on the same day, and some were separated by a little over a year (**Fig. 5b**). Near-total compensation was generally associated with very low variability, whereas partial compensation was sometimes associated with very high variability. This variability was reflected in reports about the self-motion percept. For example, when asked to rate the amount of apparent curvature in the perceived self-motion path, observers MSB and JW sometimes gave quite different responses on successive days. Observers' perceptual strategies in this task are idiosyncratic and in some cases labile. This variability presumably reflects differences in the strategies that observers use to resolve the cue conflicts that are present in these experimental conditions.

Discussion

These results suggest that accurate self-motion judgments during active head turns, and the gaze-shift compensation implied by accurate performance, are mediated by the interaction of three extra-retinal cues: vestibular canal stimulation, neck proprioception and neck efference copy. The interaction is nonlinear; for example, compensation in the passive head pursuit condition (appropriate vestibular and neck-proprioceptive stimulation) was generally quite a bit greater than the sum of the compensations measured during full-body rotation (vestibular only) and passive head stabilization (neck proprioception only). Different observers weight the three cues somewhat differently in making these judgments. It has recently been reported[11] that people also differ regarding the cues they rely on to control posture; it is possible that these two kinds of interpersonal variability are related.

These findings have important implications for physiological work on heading computation in the primate brain. Primate cortical area MSTd, the putative site of heading perception[12,13], receives both eye-movement[14] and vestibular canal[15] signals. Like our human observers, many MSTd neurons use an eye-movement signal to compensate for eye pursuit: they respond maximally to the same direction of simulated self-motion irrespective of eye movements[16]. Unlike humans, however, a similar proportion of MSTd cells also compensate for gaze shifts caused by full-body rotation, when the only available extra-retinal cue is a vestibular stimulus (K.V.S., J.A.C., D. C. Bradley & R.A.A. *Soc. Neurosci. Abstr.* **23**, 15, 1997). Although MSTd is clearly heavily involved in heading estimation, it may not embody the final stage of this computation, because many of these neurons compensate for full-body rotation, whereas human observers do not.

Methods

All experimental designs, apparati and safety procedures were approved by either the Caltech or U.C. Berkeley human subjects committee. In all conditions, observers made self-motion path judgments while monocularly viewing displays simulating linear translation at 2 m per s at a height of 1.6 m above a random-dot ground plane (in an otherwise completely dark room). At the end of each 1.5-s motion sequence, a vertical line simulating a post on the ground plane 10 m in front of the observer appeared, and observers indicated whether their self-motion path would pass to the left or right of the post. The position of the post on the ground varied along an observer-centered circle; we used a one-down, one-up psychophysical staircase procedure to find the point at which the perceived path crossed the circle (reported as the visual angle between perceived and actual crossing-points, or path error). This point was defined to be the mean of the last eight reversal points of the staircase.

There were seven pursuit conditions: simulated pursuit, eye pursuit, active and passive head pursuit, full-body rotation, and active and passive head stabilization. All of these conditions incorporated real or simulated gaze rotation about a vertical axis at constant speed. The number of observers participating in each condition (n) is shown in parentheses. During simulated pursuit ($n = 10$), the head was held fixed by a chin/head rest, and the observer fixated a stationary point above the horizon; the component of motion that would have been created by a horizontal head turn was added to the display, thereby creating the same retinal image sequence as in the real pursuit conditions. The small translation of the viewpoint caused by a head turn (not present during eye pursuit) was simulated in these displays; however, pilot data indicated that omitting this simulated translation of the viewpoint was undetectable and had no effect on observers' responses. During eye pursuit ($n = 9$), the observer turned the eye in the orbit to track a target that moved horizontally above the horizon at constant speed. In active head pursuit ($n = 6$), the head was constrained to turn from side to side by either a head/chin rest or a bicycle helmet attached to a vertical axle; head position was monitored either on-line via a potentiometer or by attaching a laser to the helmet that had to point within a target that moved across the screen. The observer had to turn the head smoothly while maintaining fixation on a target that moved with the head. Passive head pursuit ($n = 6$) was achieved by turning the vertical axle in either apparatus with a motor; observers were instructed to relax the neck muscles as much as possible, allowing the support system to take the weight of the head as well as turn it. Observers' heads were strapped in quite tightly for optimum support of the head by the apparatus. In full-body rotation ($n = 8$), the entire body was rotated about a vertical axis by a motorized chair; the head was held by a headrest attached to the chair, and the eye tracked a moving target to stay fixed in the head (canceling the vestibulo-ocular reflex, which tends to counter-rotate the eye). During passive head stabilization ($n = 5$), the body was again turned by the chair, but the headrest was attached to the ceiling to hold the head fixed in space. Active head stabilization ($n = 5$) differed in that the head was allowed to turn freely (in the helmet apparatus mentioned above), and the observer actively counter-rotated it to keep the helmet-mounted laser pointing within a stationary target. Pursuit or rotation rates varied from 0-9° per s in both directions. The retinal images were identical in all seven conditions, containing components of motion related to the simulated forward translation, to a smooth gaze rotation and (except in the case of eye pursuit) to the translation of the eye about the center of the head. When the observer's head turned with respect to the screen, the resulting drift of the center of perspective projection was taken into account. Thus, any performance differences reflect contributions of the extra-retinal cues being manipulated.

During full-body rotation and active and passive head stabilization, the motorized chair followed a trapezoidal speed profile: first, a constant-acceleration phase at 100° per s²; second, a constant-speed phase at the specified rotation rate, during which the stimulus was present and the observer responded; and finally a constant-deceleration phase at 100° per s². A control experiment verified that this vestibular stimulation was detectable during full-body rotation. In the control experiment, observers' bodies were turned while they viewed displays simulating pursuit with no forward self-motion. They adjusted the rate of simulated pursuit until the ground plane in the display appeared stationary with respect to the (invisible) room. At the highest body-rotation rates (when errors were largest in the self-motion task), the estimated gain of the vestibular com-

pensation process was significantly greater than zero; the mean across observers was 0.97 ± 0.37, indicating complete compensation.

In a second control experiment, we measured the forces between observers' heads and the apparatus during passive head pursuit. Force transducers (laminated foil strain gauges) were inserted between the observer's head (forward of the temple on either side) and the apparatus. The observer wore a headband with aluminum plates on either side of the head at the front; the force transducers pressed against these plates. The voltage across each transducer was sampled once per video frame (66 Hz), resulting in an angular sample spacing of 4.5 arcmin at a rotation rate of 5° per s and 8.2 arcmin at 9° per s. Traces were stored and analyzed off-line. Self-motion judgments were similar to those in the original passive head pursuit condition. As a baseline, we ran a condition (the 'at rest' condition) in which we attempted to achieve the greatest possible degree of passivity. In this experiment, the observer's head was deviated to a series of angles and held there by the apparatus; the force between apparatus and head was measured while the observer closed his eyes, rested his head on the chin strap and relaxed as much as possible (**Fig. 4a**). The same panel also shows the distribution of force traces obtained during all the trials of a single run of the passive head pursuit condition.

At first glance, these data suggest that the observer was actively assisting the motion. However, length–tension relationships in muscle fibers depend on the velocity of contraction or extension[17], so we should not necessarily expect the two sets of forces to be identical. We were unable to find a biomechanical model applicable to our experimental conditions from which to estimate the expected difference between these two conditions. In lieu of such a model, we attempted to determine whether the magnitude of the difference between the two sets of data affected observers' responses. First, we grouped the traces based on the observer's response on that particular trial. In this particular run, a passive head pursuit to the left at 9° per s, lack of perceptual compensation would tend to make the perceived self-motion path curve to the left. If an observer-generated force in the appropriate direction led to increased compensation (and hence a perceived path that curved less to the left), then we should expect to see more 'right' responses on trials when the measured forces deviated more from the static control experiment. No such difference was observed (**Fig. 4b**). This analysis was repeated using only the points near the midpoint of the psychometric function (that is, with 'percent right' response rates between 40 and 60%) in an attempt to partial out the effect of the probe position itself (the staircase variable) on the responses; the results of this second analysis were very similar to the first. Both observers showed similar trends at head-rotation rates of 5 and 9° per s in both directions.

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