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Primate Memory Saccade Amplitude After Intervened Motion Depends on Target Distance

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Li, Nuo, Min Wei, and Dora E. Angelaki. Primate memory saccade amplitude after intervened motion depends on target distance. *J Neurophysiol* 94: 722–733, 2005. First published March 23, 2005; doi:10.1152/jn.01339.2004. To keep a stable internal representation of the visual world as our eyes, head, and body move around, humans and monkeys must continuously adjust neural maps of visual space using extraretinal sensory or motor cues. When such movements include translation, the amount of body displacement must be weighted differently in the updating of far versus near targets. Using a memory-saccade task, we have investigated whether nonhuman primates can benefit from this geometry when passively moved sideways. We report that monkeys made appropriate memory saccades, taking into account not only the amplitude and nature (rotation vs. translation) of the movement, but also the distance of the memorized target: i.e., the amplitude of memory saccades was larger for near versus far targets. The scaling by viewing distance, however, was less than geometrically required, such that memory saccades consistently undershot near targets. Such a less-than-ideal scaling of memory saccades is reminiscent of the viewing distance–dependent properties of the vestibuloocular reflex. We propose that a similar viewing distance–dependent vestibular signal is used as an extraretinal compensation for the visuomotor consequences of the geometry of motion parallax by scaling both memory saccades and reflexive eye movements during motion through space.

INTRODUCTION

To interact with our surroundings, we must be able to accurately detect and store spatial information about objects in the environment. Indeed, we can make successive saccades to the memorized location of previously flashed targets, suggesting that the brain must construct internal representations of visual space, such that the location of objects not currently foveated can be stored and retrieved for later use. Because objects are at least initially encoded in an eye-centered reference frame (Boussaoud and Bremmer 1999; Cohen and Andersen 2002), their spatial location is no longer known whenever gaze, the position of the eyes in space, is either actively or passively redirected. To compensate for potential gaze changes and maintain a stable neural representation of the outside world, the brain must continuously adjust its internal representation of the environment using extraretinal signals. This ability, often referred to as "updating," has been demonstrated often for intervening voluntary eye movements (Hallett and Lightstone 1976; Herter and Guitton 1998; McKenzie and Lisberger 1986; Ohtsuka 1994; Schlag et al. 1990; Zivotofsky et al. 1996).

In everyday life, gaze changes relative to objects of interest also occur when our head and body rotate or translate in space. Medendorp and colleagues (2003) recently showed that updating is accurate when humans actively moved their head sideways by bending at the lower back and neck. Importantly, the amount of body displacement during translation must be weighted differently in the updating of far versus near targets, as shown in Fig. 1A, which illustrates the geometrical need for a larger eye movement for near compared with far targets during translation. This occurs because updating the stored representation of object location must anticipate the consequences of motion parallax, a geometrical property whereby near objects slip on our retina more than those on the horizon (Howard and Rogers 1995). Medendorp et al. (2003) showed that this geometrical property is taken into account by adjusting the amplitude of memory saccades during active translations and rotations. For the latter, incorporating the geometry of motion parallax is also necessary (although much smaller) when the head rotates about an axis that is different from the rotational axis of the eye, thus involving an eye translation relative to the target, as illustrated in Fig. 1B.

Extraretinal cues during the active movements in the Medendorp et al. (2003) study can arise from multiple modalities, including vestibular, proprioceptive, and efference copy signals. Are we equally capable of performing these tasks in response to gaze-in-space changes associated with passive displacements of the body, such as those occurring when riding in a car or train? Under these conditions, neither efference copies of the motor command nor neck proprioceptive signals can provide veridical information about the intervening movement, leaving the vestibular system as the main extraretinal source of motion-related information. Indeed, there is growing evidence that vestibular signals are important for path integration (Bremmer and Lappe 1999; Cohen 2000; Israel et al. 1996, 1997; Stackman and Herbert 2002) and can be used to drive voluntary eye movements (Israel and Berthoz 1989).

It is presently unknown whether vestibular signals can be used to update memory-guided eye movements during translation, similarly as previously shown for head and body rotation (Baker et al. 2003; Israel et al. 1999; Klier et al. 2005). The main goal of the present study was to investigate whether memory-guided saccades are scaled by both motion amplitude and viewing distance during passive displacements. Our results support this hypothesis, suggesting that vestibular information can be used centrally to anticipate the visual consequences of

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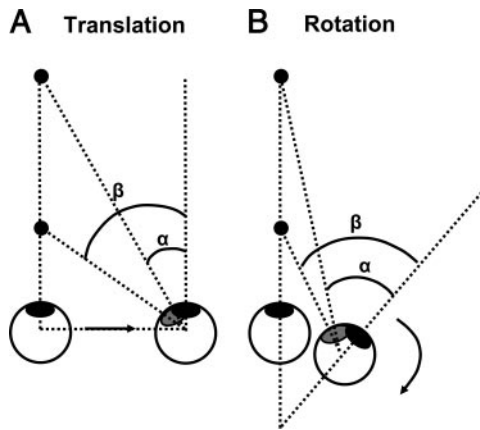
A Translation   B Rotation

FIG. 1. Schematic illustration of the geometry underlying eye movement scaling by target distance during (*A*) lateral translation and (*B*) rotation about an axis that is different from the rotational axis of the eye. Under both conditions, the eye movement required to fixate a near target is larger than that for a far target (i.e., $\beta > \alpha$).

motion parallax for spatial memory, as shown previously for low-level, reflexive eye movements (Paige and Tomko 1991; Schwarz and Miles 1991; Schwarz et al. 1989). In addition to characterizing the accuracy of the updating process for the first time during passive translations, we also quantify the properties of the version and vergence eye movements elicited during both the stationary and motion memory depth tasks. Preliminary results have been presented in abstract form (Li et al. 2004).

METHODS

Subjects

Two rhesus monkeys were chronically implanted with a head ring anchored to the skull with stainless steel or titanium screws (Angelaki 1998). To record eye movements, traditional scleral eye coils were surgically implanted under the conjunctiva of both eyes to measure horizontal and vertical eye movements. Animals were trained to perform memory-guided saccadic eye movements (Baker et al. 2003; Vogelstein et al. 2003). All surgical procedures and animal handling were in accordance with institutional and National Institutes of Health guidelines.

Experimental setup

During experiments, head-restrained monkeys sat in a primate chair that was mounted on top of a motion platform (Neurokinetics, Pittsburgh, PA), which was used to passively translate or rotate the animals. The initial fixation target was a light-emitting diode (LED) located about 1 m in front of the monkey at eye level. This "*fixation*" target, which was mounted on the motion platform, always remained at a fixed distance from the animal (head-fixed). This ensured a similar starting position of the eyes for all runs. Visual targets for the memory eye movement tasks (referred to here as "*flashed*" or "*memory*" targets) were provided by one of 5 LEDs lined up directly in front of the monkey at different distances: 12, 17, 22, 27, and 60 cm. These LEDs were mounted on a horizontal panel that was placed slightly below the monkey's eyes and secured to the floor. Thus flashed/memory targets always remained fixed to the world in these experiments and required primarily horizontal eye movements to be foveated (see *Data analyses*). Because these LEDs were placed slightly below the head-fixed far target at 1 m, small vertical eye position changes (about 4–10°) were also typically called for. The position of the monkey from the target array at the beginning and end of each run

could be manipulated using the motion platform (see *Behavioral paradigms*).

Binocular horizontal and vertical eye movements were measured using a 3-field magnetic coil system (CNC Engineering, Seattle, WA). The animal's performance during these memory tasks was monitored on-line using behavioral windows for both version and vergence. Instantaneous version and vergence positions were calculated from the left (L) and right (R) eye positions, as (R + L)/2 and L − R, respectively. Eye-movement signals were low-pass filtered using 6-pole Bessel filters at 200 Hz. The data were digitized at 833.3 Hz with 16-bit resolution and stored for off-line analysis. A custom-written script in the Spike2 software controlled stimulus presentation and data-acquisition hardware (CED Power 1401; Cambridge Electronic Design, Cambridge, UK).

Behavioral paradigms

Animals were trained to perform memory saccades under 3 conditions, which will be referred to as "stationary," "translational motion," or "rotational motion" tasks. These 3 types of memory tasks were typically randomly interleaved within blocks of trials that were collected on multiple experimental days. The general outline of the tasks is illustrated in Fig. 2. All trials began with the onset of the fixation target in a dimly illuminated room (interval 1). During continued fixation of the 1-m fixation target (±2° version and ±0.75° vergence windows) for >500 ms, one of the closer, world-fixed LEDs flashed for 200 ms (interval 2). Then, during a variable delay period lasting 750–1,750 ms (interval 3), animals either remained stationary ("stationary" task) or were moved ("motion" tasks). This movement, which started within 50 ms after the flash, lasted 500 ms, was completed before the fixation target was turned off, and included either a 5-cm rightward/leftward translation or a 10° leftward/rightward rotation (with the axis of rotation 7.5 cm behind the eyes). All motions had a trapezoidal velocity profile with peak velocities of 10 cm/s and 20°/s for translation and rotation, respectively. For translational trials, peak linear acceleration was 1.25 m/s². During the motion, animals were trained to suppress their VOR with eye position being maintained within the specified behavioral fixation windows.

The room lights were turned off immediately after the flash, leaving the animal in complete darkness (other than the head-fixed fixation target). Thus no visual cues were available to the light-adapted animal to indicate the direction and amplitude of the interleaved movement. Turning off the fixation target provided the cue for the monkey to look at the remembered location of the previously flashed target (interval 4). The animal had to make an eye movement to that location and hold eye position within larger behavioral windows (±8° in version and ±3° in vergence) for 1 s, before the memory target and room lights were turned on again (interval 5), allowing the monkeys to make a corrective eye movement (if necessary) to the relighted target. The animal was required to fixate (±2° for version and ±0.75° for vergence) the relighted LED for 1 s before receiving a juice reward. This 1-s fixation duration was imposed to allow sufficient time for a typically slowly changing vergence response (Maxwell and King 1992; Zee et al. 1992).

The duration of individual trials varied from trial to trial (about 4–7 s) as a result of the variable delay period and variable reaction times for memory-guided and corrective eye movements (including the required 1-s memory and postmemory fixation periods once the eyes fell inside the respective behavioral windows). If either the version or vergence eye position fell outside the specified behavioral windows at any time during the task, the trial was aborted and the data were discarded.

Motion and stationary trials differed in the motor error needed to generate accurate memory-guided eye movements. For stationary trials, the required memory eye movement was toward the location of the flash, and thus motor error was approximately equal to retinal error (Klier and Crawford 1998) and no updating was required. In contrast,
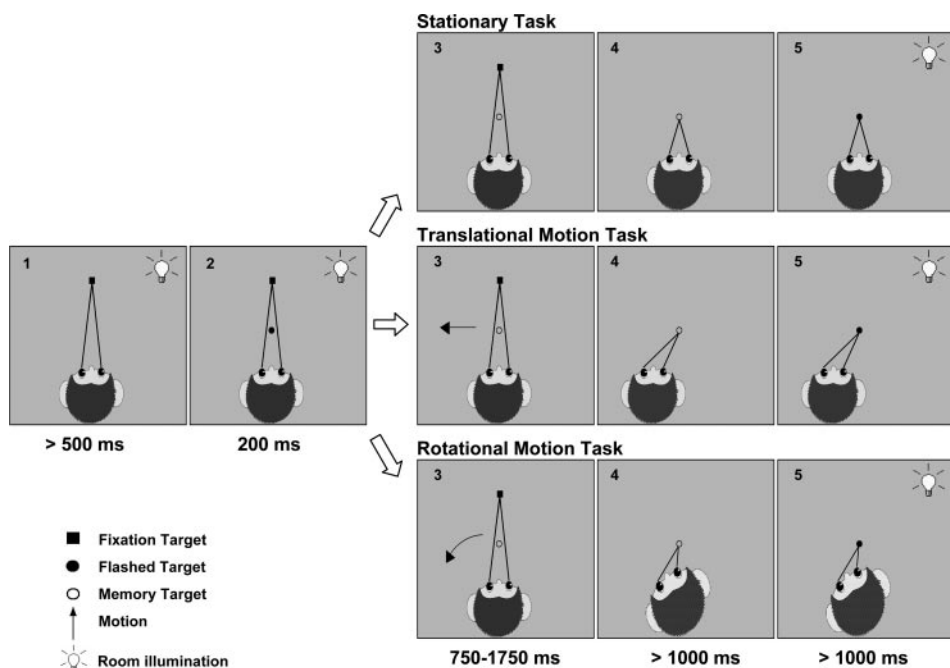
FIG. 2. Experimental paradigms for stationary and motion tasks. Animal began by fixating a head-fixed central target in an illuminated room (interval 1). After the flash of a second, space-fixed, target (interval 2), the room lights were turned off while the monkey maintained fixation on the initial target for an additional time period that varied from trial to trial (interval 3). Offset of the central target provided the cue for the animal to make an eye movement toward the remembered target location (interval 4). Each trial terminated with a corrective eye movement when the memory target (and room lights) were turned back on (interval 5). Motion trials (*middle* and *bottom*) differed from the stationary task (*top*), as the animal was moved (translated or rotated) to the left or the right during the delay period (interval 3). Although retinal information alone is sufficient to specify the memory eye movement for the stationary task, extraretinal motion cues would be necessary to update the memorized spatial target location for the motion tasks.

because at the end of the rotational/translational motion trials, animals ended up at a different angle (and slightly different distance) relative to the flashed target, the retinal location of the flash was no longer appropriate as a motor error for the memory eye movement. Instead, for the monkeys to perform this task accurately, extraretinal sensory cues related to the intervened movement were required to compute the motor error for the memory eye movement.

To directly compare memory eye movements for motion trials (where updating was necessary) with those for stationary trials (where no updating was needed), data for the stationary task were gathered at all initial and final positions of the motion trials. This included a total of 25 combinations, corresponding to the 5 flashed targets at any one of 5 positions relative to the target array: original orientation (with memory targets directly in front), rotated 10° rightward/leftward, or translated 5 cm rightward/leftward of the target array. With animals in the original orientation and flashed targets directly in front, the horizontal eye movement called for during the memory period was a purely vergence response (depth change). In contrast, when the eye movements were made from the rotated or translated stationary positions, changes in both the version (direction change) and vergence (depth change) were necessary.

Animals were extensively trained with this task for longer than 3 months. To verify that a trial-by-trial sensorimotor transformation was performed during these spatial memory tasks, trained animals were also tested with additional experimental blocks that included novel motion amplitudes (but no stationary trials). For these new protocols, 3 translation (3, 4, or 5 cm) and 3 rotation (5, 8, or 10°) amplitudes were used (for a total of $12 \times 5 = 60$ conditions). Because we wanted to investigate how accurate these eye movements were, and to avoid excluding runs where memory performance was poor, no behavioral window was imposed for the memory period during these variable motion amplitude blocks. Thus all runs in which the monkeys successfully ignored the flash and refixated the memory target after it was relighted were rewarded and saved for off-line analysis.

Finally, data were also collected during interleaved rotation and translation motion trials to the 17-, 22-, 27-, and 60-cm targets for 2 different locations of the initial fixation, head-fixed LED: one at 1 m (similar as in all other experimental protocols), the other at 12 cm. This additional protocol aimed at comparing the accuracy of updating and the scaling of the memory saccade amplitude by distance, separately for convergent and divergent eye movements.

Data analyses

Only successful trials (with reward delivery) were analyzed off-line using Matlab (The MathWorks, Natick, MA). Eye movements were calibrated using a daily fixation task with positive eye position corresponding to upward and rightward directions. A custom-written script allowed the experimenter to examine each trial manually by plotting the horizontal and vertical positions of each eye, as well as horizontal version and vergence. A semiautomatic procedure was used to identify saccades when eye velocity (resultant of horizontal and vertical components) exceeded (or fell below) 25°/s. Memory responses were aligned at saccade onset and averaged across trials.

For each experimental run, 4 sets of eye position values were computed by averaging eye position over 20-ms time intervals: *1*) The *initial fixation* was computed 50 ms before the head-fixed target was turned off. *2*) The *endpoint of the memory saccade* was computed 50 ms after the end of the memory saccade. *3*) Because of an often slowly changing vergence angle, the *end of the memory period* (also referred to here as *memory eye position*) was computed 50 ms before the reillumination of the memory target (i.e., 950 ms after the eyes were within the specified memory windows; see above). *4*) For a comparison of the memory-guided with the visually guided movement, the *postfixation* eye position was also computed after the memory target was relighted at the end of the trial. These postfixation data were used as the "ideal" eye movement necessary to foveate the target.

The changes in horizontal version (direction) or vergence (depth) eye position after the memory-guided eye movement were then calculated as the difference between the endpoint of the saccade or the memory period and the initial fixation position. These values were then compared with the required change in eye position, computed as the difference between the postfixation and the initial fixation values. These variables defined the "accuracy" of memory-guided eye movements and correspond to a vergence/version generalization of what has been referred to as "systematic error" in previous studies (White et al. 1994). In addition, to estimate the variability of memory-guided eye movements, we computed "variable errors" defined as the SD of version and vergence endpoints about their mean. Because the vertical saccadic component was small (see *Experimental setup*), analyses have focused on horizontal eye movements.

Relationships between variables were quantified using linear regressions, obtained by minimizing either the vertical offset (Regress

function of Matlab) or the perpendicular offset of the data to the line (using a nonlinear least-square algorithm based on the interior-reflective Newton method; Coleman and Li 1994, 1996). The latter analysis was used for independent variables (e.g., Fig. 9), with 95% confidence intervals computed using bootstrapping with replacement thus, the confidence intervals were typically asymmetric. Other comparisons between variables were made using ANOVA.

RESULTS

Memory eye movements for the stationary task

Monkeys were trained to perform memory-guided eye movements to targets flashed at different distances, as illustrated in Fig. 3. For example, the trial shown in Fig. 3*A* started with fixation of a far (1 m), head-fixed, central LED, while a world-fixed target at a distance of 12 cm was briefly flashed (Fig. 3; intervals 1 and 2). Then, as soon as the fixation target was turned off (Fig. 3; end of interval 3) and while stationary in complete darkness, the monkey made an eye movement toward the memorized world-fixed target location (Fig. 3; interval 4). Because the central fixation and flashed targets were located at different depths, the two eyes did not move equally. In fact, because the flashed target in this example was in the midsagittal plane, there was an opposite change in the horizontal position of the two eyes, resulting in a large vergence angle change (Fig. 3*A*, *last row*). This change in vergence for near targets was typically less than expected from a visually guided eye movement, as illustrated by the corrective movement that brought the eyes closer to the target when it was turned back on (Fig. 3*A*, interval 5). For targets flashed further away from the animal, the observed change in vergence was smaller (e.g., for a 60-cm target; Fig. 3*B*).

These examples illustrate that subjects took into account the retinal disparity of the flash and elicited vergence memory eye movements in darkness, as required by the distance of the flashed target. However, vergence did not always reach steady-state values during the 1-s memory period before the reillumination of the peripheral target. This is illustrated in Fig. 4*A*, which plots the mean (±SE) for all stationary trials to centrally located flashed targets at distances of 12, 17, 22, 27, and 60 cm, separately for each animal (*top* and *bottom traces*). In contrast, visually guided vergence reached higher steady-state values faster (Fig. 4*B*). Similar observations were also made for memory eye movements to eccentric target locations, the main difference being that changes in both the horizontal version
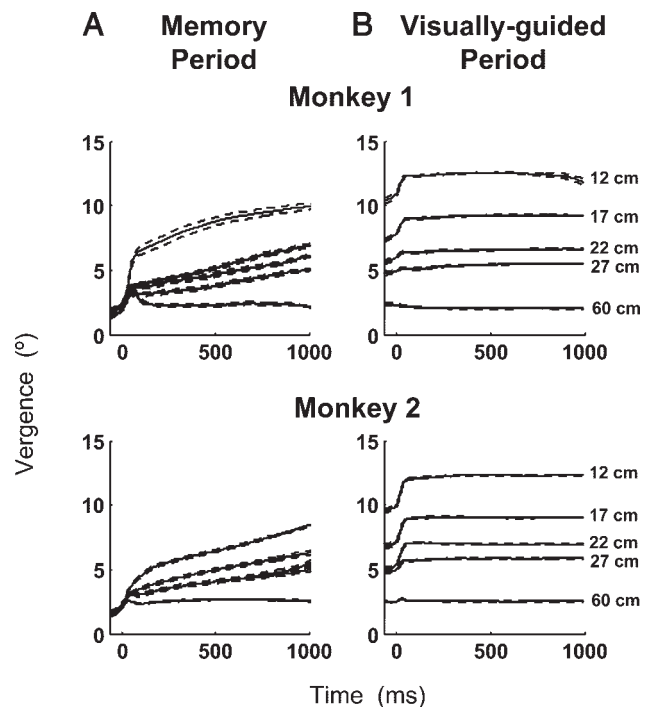

FIG. 4.   Stationary task: mean (±SE) of (*A*) the memory vergence elicited for each of the 5 central targets flashed at different distances (12, 17, 22, 27, and 60 cm), as well as (*B*) the corrective eye movements made after the flashed target was turned back on. Data are shown separately for each animal (*top* and *bottom*). To compute the averages, individual runs were aligned at saccade onset for each period (*time = 0*). Notice that vergence often continued to increase throughout the memory period for near targets, with values at the end of the memory period being typically less than required (see corrective movements after the memory target was turned back on). Because the flashed targets were not exactly in-between the eyes and because all saccades had a vertical component (see METHODS), these data do not represent symmetric vergence responses. Number of trials ranged between 28 and 52 (animal 1) and 40 and 131 (animal 2).

(conjugate) and vergence (disjunctive) components of the eye movement were called for.

Memory endpoints were characterized by higher variability than visually guided movements [factorial ANOVA, $F(270,1) = 415$, $P < 0.001$]. How accurate memory eye movements were in comparison to postfixation values (i.e., the visually guided eye movement made after the memory target was turned back on at the end of the trial) is illustrated in Figs. 5 and 6. We used linear regressions to relate the memory eye
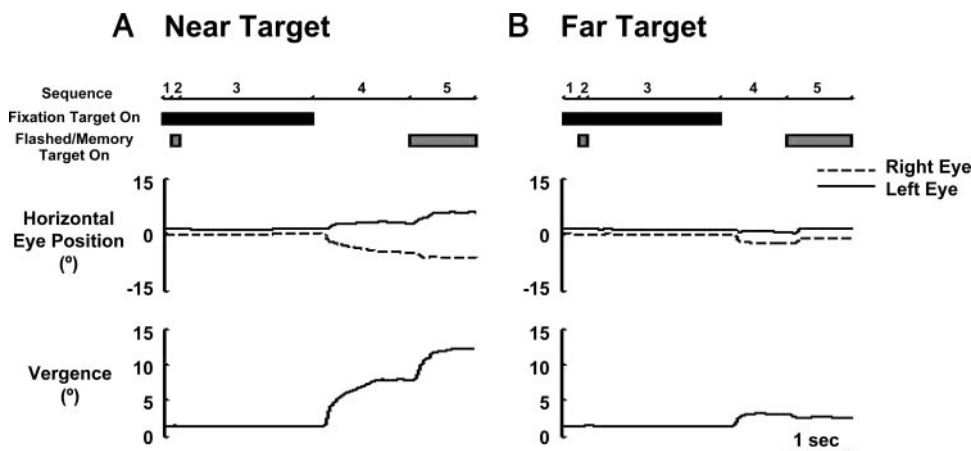

FIG. 3.   Stationary task: examples of memory eye movements to targets flashed at different distances: (*A*) 12 cm and (*B*) 60 cm. In both examples, the flashed target was approximately in-between the eyes, and thus mainly a vergence eye movement was generated. Notice that the larger the disparity error of the flashed target, the larger the memory-evoked vergence eye movement.
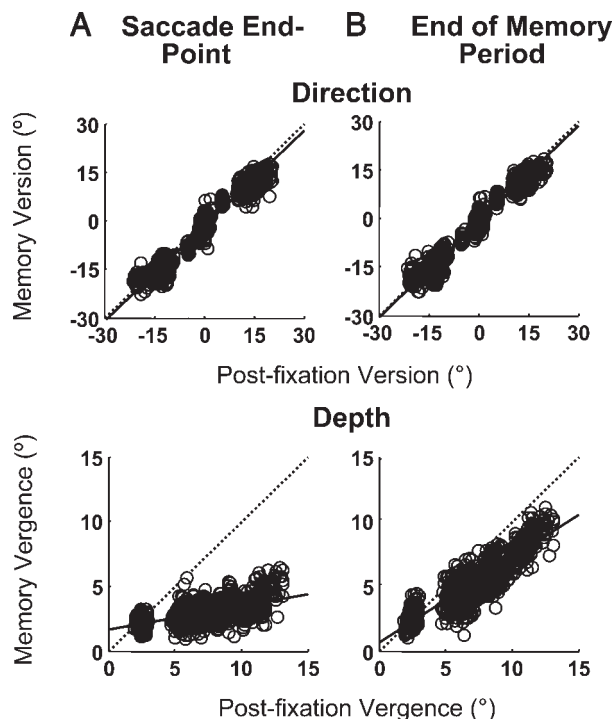
A   Saccade End-Point

B   End of Memory Period

Direction

Depth

FIG. 5. Comparison between memory and postfixation eye movements for stationary trials. *Top panels*: changes in direction (version). *Bottom panels*: changes in depth (vergence). Memory performance was evaluated by the eye position measured (*A*) 50 ms after the memory saccade, and (*B*) 50 ms before the reillumination of the memory target. Each symbol corresponds to one of 1,190 successful runs from animal 2. Solid lines are linear regressions (parameters are included in Table 1).

movement direction (version) and memory eye movement depth change (vergence) to the actual direction and depth of the memory target. In general, the direction of the target was better compensated for than was its corresponding depth. Specifically, the conjugate component of the memory-guided eye movement was accurate immediately after the memory saccade. However, this was not the case for the disjunctive component. This property can already be seen in the examples of Fig. 4*A*, where the vergence angle continued to increase during the memory period.

To quantify this difference, the memory performance was evaluated by measuring eye position 50 ms after the memory saccade, as well as 50 ms before the reillumination of the memory target (end of memory period). These values, from all stationary trials in animal 2, are plotted versus the corresponding postfixation eye position in Fig. 5, *A* and *B*, respectively. Regression analysis results for both animals are summarized in Table 1. The regression for either memory values was always statistically significant (Table 1), but only for version were the regression line slopes close to unity at both the saccade endpoint and the end of the memory period. In contrast, immediately after the saccade, memory vergence was only on average 19–38% of the respective visually guided eye movement. This correlation improved to 66–76% at the end of the memory period (Fig. 5; see also Table 1).

The relationship between memory and postfixation vergence was independent (linear regression confidence interval, $P > 0.05$) of whether there was a simultaneous change in horizontal version (as a small vertical saccade was always present because of the different vertical elevations of the far fixation and

flashed near targets; see METHODS). This is illustrated in Fig. 6, which plots, for both animals, the average memory vergence as a function of the respective visually guided vergence, separately for the 5 targets centered in-between the eyes and the 20 targets at eccentric locations (filled vs. open symbols). Even at the end of the memory period, memory vergence fell short of the required visually guided vergence, as if the near targets were seen further away than where they actually were. All subsequent analyses focus on the latter memory period values, which reflect the slower change in vergence angle.

Memory eye movements for the motion tasks

For the stationary trials, results of which have been summarized above, the required memory eye movement was toward the location of the flash and no updating was required. In contrast, for *motion trials*, animals were either translated 5 cm or rotated 10° to the right/left during the delay period, such that the spatial location of the memory eye movement goal differed from the location of the flash (Fig. 2). Examples of two such motion trials, with the flash at 12 and 60 cm and a 5-cm leftward displacement during the delay period, are illustrated in Fig. 7. If the animal did not update the goal of the memory eye movement, a purely vergence response would be expected, as illustrated under identical stationary conditions in Fig. 3. In contrast, for the memory eye movement to be appropriate for the now eccentric location of the memory target, a conjugate rightward horizontal eye movement, whose amplitude should depend on flashed target distance, would be expected to accompany the change in vergence. Indeed, despite an identical displacement, the memory saccade depended on the distance of the flash: its amplitude was larger for near than far targets (Fig. 7, *A* and *B*).

Mean (±SE) of the horizontal direction (version) and depth (vergence) changes for translational motion trials to flashed targets at distances of 12, 22, and 60 cm have been compared with the corresponding final-position stationary trial data, randomly interleaved within the same experimental blocks, in Fig. 8. As illustrated by comparing *A* and *B*, horizontal saccade amplitude for the translational motion task scaled with target distance, although less than in the corresponding stationary trials.
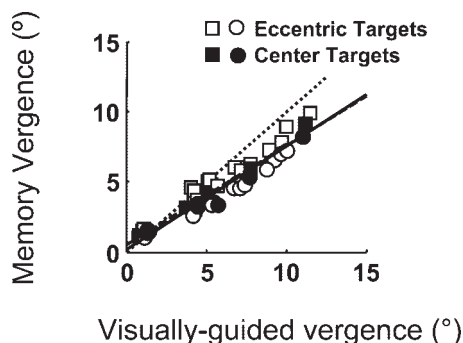
FIG. 6. Relationship between memory and postfixation vergence for central and eccentric targets. Memory vergence was measured 50 ms before the reillumination of the memory target. For each of the two animals (shown with circles and squares), filled symbols represent averages for the 5 targets centered between the two eyes, whereas open symbols are the averages for each of the 20 targets at eccentric locations. Solid and dashed lines illustrate linear regressions, with slopes (±95% confidence intervals): central targets, 0.73 ± 0.11, $R^2 = 0.97$; eccentric targets, 0.71 ± 0.07, $R^2 = 0.92$.

TABLE 1. *Stationary trials: linear regression parameters for memory eye position as a function of postfixation values*

Subject			Slope ± 95% CI	Intercept ± 95% CI	R^2	n
Monkey 1	Direction	Saccade end-point	0.81 ± 0.01	−2.04 ± 0.15	0.94**	1,041
		End of memory period	1.00 ± 0.01	−0.33 ± 0.15	0.95**	
	Depth	Saccade end-point	0.38 ± 0.02	0.97 ± 0.18	0.51**	
		End of memory period	0.76 ± 0.02	0.87 ± 0.14	0.86**	
Monkey 2	Direction	Saccade end-point	0.98 ± 0.01	−1.62 ± 0.12	0.96**	1,190
		End of memory period	0.98 ± 0.01	−1.00 ± 0.12	0.96**	
	Depth	Saccade end-point	0.19 ± 0.01	1.62 ± 0.09	0.39**	
		End of memory period	0.66 ± 0.02	0.68 ± 0.12	0.84**	

CI, confidence intervals. Asterisks illustrate statistically significant regressions ($P < 0.001$).

We measured the eye movement changes at the end of the memory period for both stationary and motion trials. The mean (±SD) version and vergence memory eye position from translational motion trials are plotted versus the corresponding data from the final position stationary trials in Fig. 9A. If motion-related, extraretinal information changed the goal of the saccade away from the retinal error of the flash, as required by the world-fixed location of the memorized target, data should fall along the unity-slope line when plotted versus memory eye position from the final-position stationary trials. Indeed, significant correlations were seen, although regression slopes were lower than unity (Table 2). For animal 1, the regression line had a slope of 0.63, which was not significantly different from unity (95% interval included the value of 1.0; Table 2). The regression line slope for animal 2 (0.43) was smaller (95% interval excluded the value of 1.0; Table 2). Thus although extraretinal motion information was taken into account, the scaling of the amplitude of the horizontal eye movement was incomplete for the nearest flash locations (Fig. 9, green, red, and orange symbols). Similar results were obtained for rotational motion trials (Fig. 9B; Table 2), where a small translation of the eyes relative to the target was also present (because the axis of rotation was 7.5 cm behind the eyes; see schematic of Fig. 1B and Crane and Demer 1998; Hine and Thorn 1987; Snyder and King 1992; Wei and Angelaki 2004).

When the dynamics of the motion task memory saccades were compared with those of the stationary task, only latency differences were found. Specifically, the memory saccade latency was typically longer for the motion task than that for the stationary task [Table 3, factorial ANOVA, $F_{(5,477,1)} = 228$, $P < 0.001$]. In addition, motion trials were also characterized by higher variability than stationary runs [factorial ANOVA, $F_{(180,2)} = 228$, $P < 0.001$]. In contrast, the main sequence relationship between peak velocity and saccade amplitude was not altered, as illustrated in Fig. 10 (see also Table 3).

In these experiments, all memory eye movements were made from a far to a near target, a condition where there exists a direct covariation between how close the memory target is (and thus how large the horizontal saccade amplitude should be) and the intensity of the ongoing convergence response. To exclude the possibility that horizontal saccade scaling by distance is solely attributed to the ongoing convergence, data were also collected in a second experiment, where convergence (head-fixed, fixation target at 1 m) and divergence (head-fixed, fixation target at 12 cm) trials were randomly interleaved with flashed targets at 17, 22, 27, and 60 cm. Unlike the convergence trials, in the case of divergence eye movements, the larger and more intense the divergence response, the smaller the memory saccade amplitude should be.

Similar saccade sizes were evoked during convergence and divergence trials [ANOVA, $F_{(1,651,1)} = 1.56$, $P \gg 0.05$]. When motion data were plotted versus the respective stationary data (as in Fig. 9), regression line slopes were larger for convergence than for divergence trials (mean ± 95% confidence intervals were 0.84 ± 0.60 and 0.50 ± 0.40, respectively) (Fig. 11, black and gray lines). Although slopes were different, confidence intervals were overlapping, suggesting that updating performance was not statistically different between convergence and divergence trials. Therefore the memory update appears to be invariant with the depth location of the first target, although the exact saccade scaling by distance might depend on the direction and intensity of the ongoing vergence.

Finally, a third experimental manipulation was used to verify that animals performed an on-line sensorimotor transformation, rather than an arbitrary stimulus-response mapping.
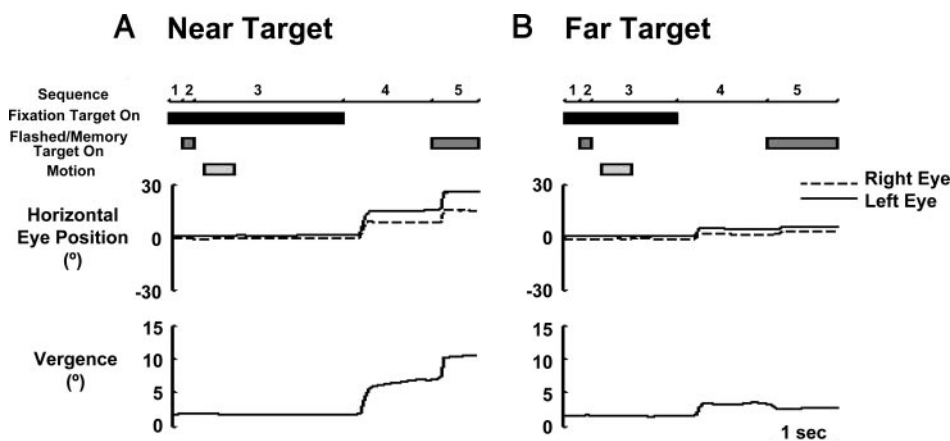

FIG. 7. Translational motion task: examples of memory eye movements to targets flashed at different distances: (A) 12 cm and (B) 60 cm. Flashed target was in-between the eyes (exactly the same as in Fig. 3), but the 5-cm leftward motion required that, in addition to vergence, the animal also make a conjugate rightward eye movement (compare with Fig. 3, where only vergence changed). Notice that the memory-guided eye movement was scaled by distance, although less than required (see corrective movement after target was turned back on).
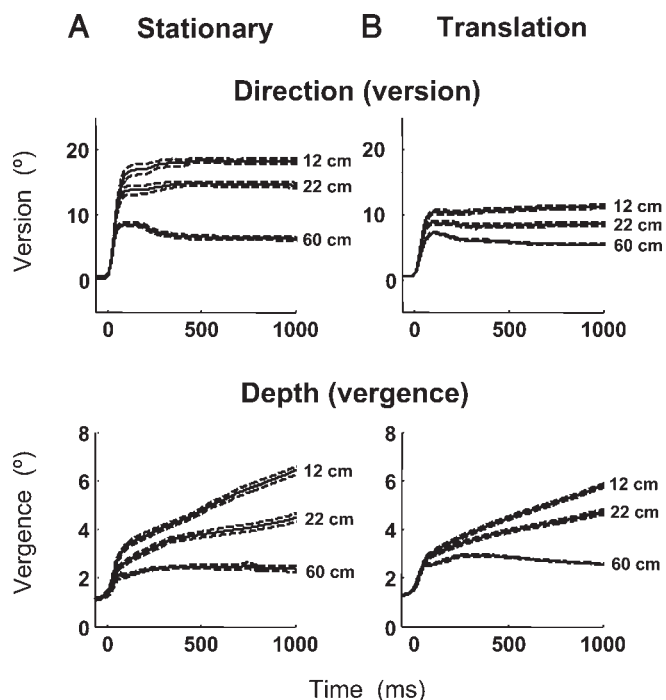
A Stationary   B Translation

Direction (version)

Depth (vergence)

Time (ms)

FIG. 8. Comparison between (*A*) stationary and (*B*) translational motion tasks: mean ($\pm$SE) of the memory horizontal version and vergence eye movements elicited for each of 3 targets flashed at different distances (12, 22, and 60 cm). To compute the averages, individual runs were aligned at saccade onset (*time = 0*). Notice that horizontal saccade amplitude scaled with distance for the translational motion task, but not as much as in the final position stationary task. Data from animal 2 for a 5-cm leftward translation.

Accordingly, animals were also tested with additional blocks, which included multiple motion amplitudes randomly interleaved within the same experimental sessions. For these multiple amplitude blocks, no behavioral window was imposed for the memory period to avoid excluding runs where memory performance was poor. Using this new task, the monkeys' performance accuracy did not change as a function of time (linear regression, $P \gg 0.05$ in 53/60 conditions; $P > 0.01$ in 60/60 conditions), a result that would argue against a motor learning explanation for the animals' performance (see DISCUSSION).

Because stationary condition trials were not tested in these blocks, mean values of the memory saccades for translational and rotational motion trials were plotted as a function of the inverse distance of the flash, as shown in Fig. 12, *A* and *B*. Monkeys compensated for both the actual distance of the flash and the amplitude of the imposed motion [factorial ANOVA, $F(1,790,4) = 300$ for *translation*, $F(1,801,4) = 90$ for *rotation*, $P < 0.001$ for *both*]. These relationships were quantified using linear regression (Fig. 12, solid lines). Superimposed in the figure is the ideal performance that would correspond to the different motion amplitudes (Fig. 12, dashed lines). It is obvious by comparing the solid and dashed lines of the same color that, following translational updating, the evoked memory saccades: *1*) scaled less with inverse distance than expected according to the geometry and *2*) did not asymptote to zero saccade amplitude at an inverse viewing distance of zero (i.e., viewing at infinity; Fig. 12*A*).

These results for translational motion trials are summarized in Fig. 13*A*, which plots the slope ratio (with a value of unity corresponding to a perfect dependency on distance) as a function
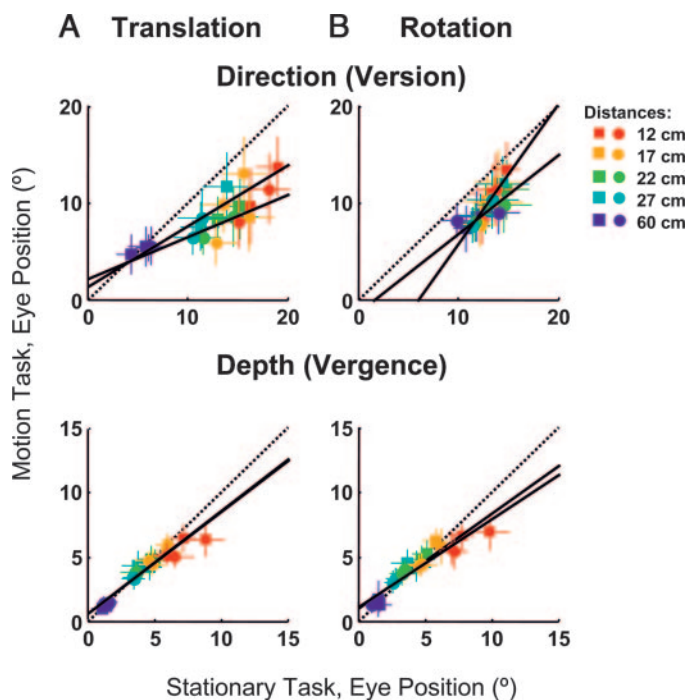
A Translation   B Rotation

Direction (Version)

Depth (Vergence)

Stationary Task, Eye Position (°)

FIG. 9. Updating accuracy for (*A*) the translational and (*B*) the rotational motion tasks. Amplitude of version and vergence eye movements made during the memory period for motion trials (ordinate) are compared with the respective values from interleaved final position stationary trials (abscissa). For perfect updating (i.e., in terms of both displacement amplitude and viewing distance), data should fall along the unity-slope (dotted) line when plotted vs. the respective final position values. Data shown are means ($\pm$SD), separately for each of the 5 distances (red, orange, green, cyan, and blue symbols) and each animal (circles and squares). Note that responses during both motion directions have been plotted as absolute (positive) values. Solid lines illustrate linear regressions, plotted separately for each animal's data.

of the respective *y*-axis intercept. Both the regression line slopes and *y*-intercepts were significantly different from ideal values, as seen from the fact that 95% confidence intervals (error bars in Fig. 13) excluded the values of 1 (for slope) and 0 (for *y*-intercept). Thus in contrast to the geometrical expectation that the magnitude of memory saccades should be zero for a target of visual infinity, the *y*-intercept for all regression lines in both animals was significantly different from zero, whereas slopes were smaller than what would have been expected based on geometry. As a result, the

TABLE 2. *Regression slopes and 95% CI for memory eye position from motion trials plotted as a function of the respective values from stationary tasks performed at the same final position (e.g., Fig. 9)*

Subject		Slope	95% CI	R^2
Translation				
Monkey 1	Direction	0.63	[0.46, 1.04]	0.83*
	Depth	0.73	[0.43, 1.08]	0.86*
Monkey 2	Direction	0.43	[0.26, 0.70]	0.72*
	Depth	0.68	[0.50, 0.94]	0.93*
Rotation				
Monkey 1	Direction	1.43	[1.11, 1.78]	0.91*
	Depth	0.80	[0.45, 0.99]	0.90*
Monkey 2	Direction	0.82	[0.39, 1.73]	0.53*
	Depth	0.79	[0.54, 1.00]	0.93*

Asterisks illustrate statistically significant regressions ($P < 0.01$).

TABLE 3. *Mean latency and peak velocity/saccade amplitude values of the memory saccades*

		Stationary Task	Translational Motion Task	Rotational Motion Task
Monkey 1	Latency	273 ± 95 ms	328 ± 99 ms (**)	305 ± 97 ms (**)
		n = 841	*n* = 632	*n* = 701
	Peak velocity/saccade amplitude	12.4 ± 0.6°/s/°	11.0 ± 0.5°/s/° (*)	11.5 ± 0.5°/s/°
Monkey 2	Latency	235 ± 66 ms	265 ± 65 ms (**)	262 ± 63 ms (**)
		n = 874	*n* = 1,272	*n* = 1,161
	Peak velocity/saccade amplitude	14.7 ± 0.6°/s/°	14.6 ± 0.3°/s/°	14.9 ± 0.3°/s/°

Values are means ± SD. Double asterisks in parentheses illustrate statistically significant differences for each of the motions compared with the stationary task (factorial ANOVA, $P < 0.001$). The peak velocity/saccade amplitude relationships are summarized by the regression line slopes (±95% CI). An asterisk in parentheses illustrates the only one motion condition where slopes were different from those in stationary trials (nonoverlapping CI). Data computed for the 5-cm (translation) and 5° (rotation) trials (where final position conditions were identical to those in stationary trials).

memory eye movements undershot near targets. For rotational motion trials where the expected dependency on target distance is smaller and the distance-independent *y*-intercept is equal to rotation amplitude (Fig. 13*B*, colored, vertical dotted lines), data were closer to ideal performance.

DISCUSSION

These results illustrate that nonhuman primates can adjust the amplitude of memory-guided eye movements after intervened passive motion consisting of either translation or rotation. We have also shown here that the computation of the memory saccade motor error takes into account not only the nature (i.e., rotation/translation) and amplitude of motion, but also the distance of the memorized target. However, we also found that this scaling of primate memory saccades by target distance was less than geometrically required for near targets, particularly for divergence tasks. The less-than-ideal slopes could be a consequence of an erroneous estimate of distance because memory vergence undershot the visually guided vergence during the stationary memory task (Figs. 5 and 6). In the following, we will first discuss reasons for underperformance of the memory vergence, then consider the possibility that these behaviors might represent a learned or adaptive behavior and finally speculate about the nature of extraretinal signals for this visuospatial updating process.

Neural estimate of target distance: origin of vergence errors during the stationary spatial memory task

We observed systematic and consistent errors in memory-guided vergence during the stationary spatial memory task. These results in monkeys are quantitatively similar to what was previously shown in human subjects (Medendorp et al.

2003). In the human experiments, targets were flashed in complete darkness, unlike the present experiments where the room was dimly illuminated during the time of the flash. Yet, under both conditions, memory vergence was less for near targets, compared with the visually guided vergence position acquired when the target was turned back on at the end of the trial. Because memory-guided vergence was accurate for far targets (Fig. 6), we consider unlikely that these errors arise from a range effect (Kapoula 1985; Kumar et al. 2003).

The sources of both the systematic and variable errors in memory-guided eye movements have been investigated for saccades on a frontoparallel plane (i.e., without associated changes in vergence). Based on the results from such studies, it is unlikely that significant errors may arise from the deterioration of spatial memory. For example, the temporal deterioration for memory-guided saccades in the frontoparallel plane occurs only for much longer delay times than those used in the present experiments (Gnadt et al. 1991; Ploner et al. 1998; White et al. 1994). Although it was originally proposed that the errors are introduced during the transformation from a perceptual memory of object location to a memory of the intended eye movement (Gnadt et al. 1991), there is increasing evidence that the systematic errors associated with the accuracy of conjugate saccades are introduced in the motor output downstream from the superior colliculus (Stanford and Sparks 1994) and downstream from the storage of remembered target location (Opris et al. 2003). Because the neural control of conjugate saccades and vergence eye movements are at least partly distinct (Gamlin 1999; Mays and Gamlin 1995; but see Zhou and King 1998), these conclusions on memory-guided saccades on a frontoparallel plane are not easily transferable to the vergence component of memory-guided eye movements.
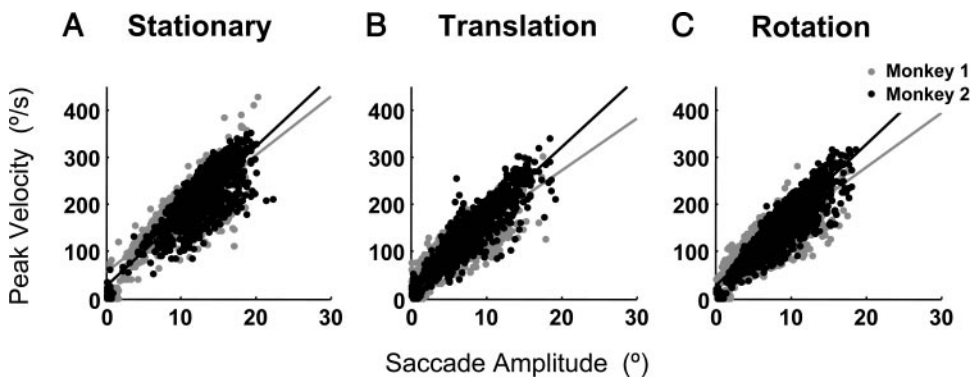

FIG. 10. Main sequence of memory saccades for (*A*) the stationary task, (*B*) the translational motion task, and (*C*) the rotational motion task. Solid gray and black lines illustrate linear regressions for the data from animals 1 and 2, respectively. Relationship between peak velocity and saccade amplitude did not change for stationary and motion conditions (Table 3).
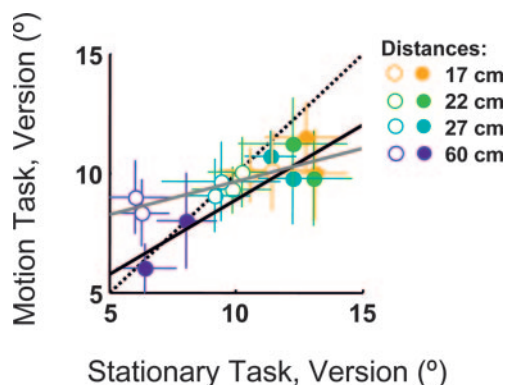
FIG. 11. Updating accuracy for convergence (far → near) and divergence (near → far) eye movements. Horizontal saccade amplitude for translational motion trials (ordinate) are compared with the respective values from interleaved final position stationary trials (abscissa). For perfect updating, data should fall along the unity-slope (dotted) line (as in Fig. 9). Data shown are means (±SD) of interleaved convergence (filled symbols) and divergence (open symbols) trials, plotted separately for each distance (orange, green, cyan, and blue symbols). Note that responses during both motion directions have been plotted as absolute (positive) values. Solid (dashed) lines illustrate linear regressions (±95% confidence intervals). Data from animal 2.

Vergence errors could be the result of a perceptual mislocalization of the distance of the target. This issue has been studied extensively with pointing movements, where similar errors are found (Berkenblit et al. 1995; Foley 1985; Soechting and Flanders 1989a). Such distance errors in pointing have been attributed either to nonlinear distortion of perceptual space (Wolpert et al. 1994) or to the underlying sensorimotor
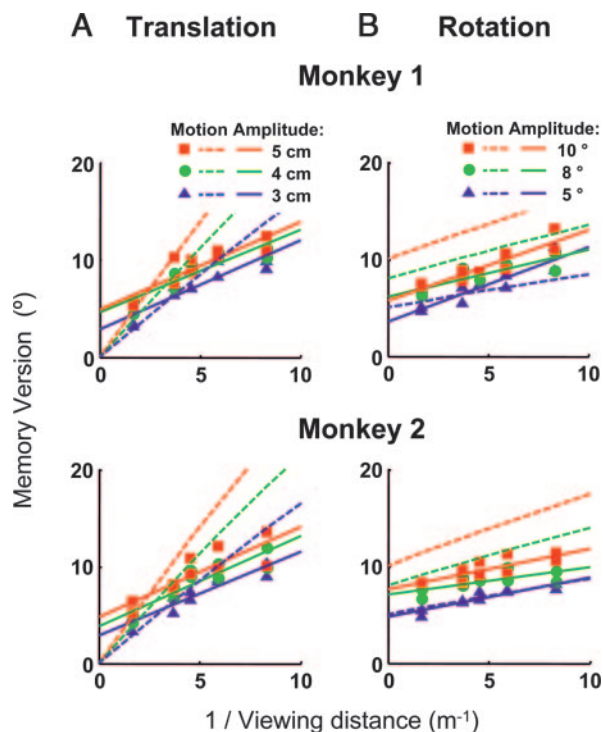

FIG. 12. Scaling of the amplitude of memory saccades as a function of inverse viewing distance. Memory eye movements for (A) translational or (B) rotational motion trials have been plotted vs. the inverse of target distance separately for data from animal 1 (top) and animal 2 (bottom). Data shown are means, calculated separately for each of 3 amplitudes (red squares, green circles, and blue triangles). Dotted lines illustrate geometrically appropriate updating.
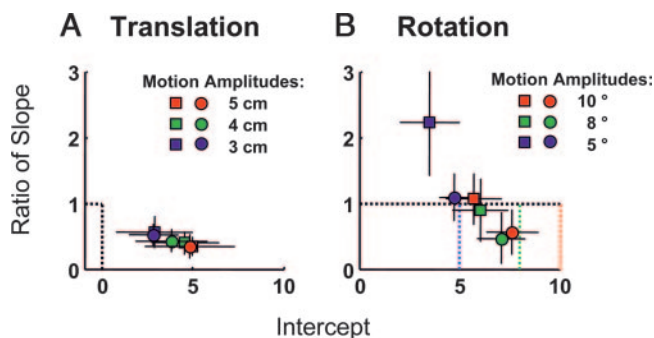

FIG. 13. Less-than-ideal dependency on the distance of the flash for (A) translational and (B) rotational motion trials. Symbols illustrate the regression line parameters from Fig. 12 (ordinate: slope ratio relative to the geometrically appropriate viewing distance dependence slope; abscissa: *y*-intercept of the regression). Error bars represent 95% confidence intervals. Dotted lines illustrate the respective geometrical expectations, including a unity-slope ratio (for both motion tasks) and a zero (for translation) or amplitude-dependent *y*-intercept (for rotation). Parameters have been computed separately for each animal (circles and squares) and each of 3 amplitudes (red squares, green circles, and blue triangles).

transformations (Soechting and Flanders 1989a,b). Similar errors of perceived distance have also been reported during walking (Philbeck and Loomis 1997), as well as in the scaling of the translational vestibuloocular reflex (TVOR) by a neural estimate of target distance (Angelaki et al. 2000; Schwarz and Miles 1991; Telford et al. 1997; Wei and Angelaki 2004; Wei et al. 2003). Because of such extensive evidence that, at least for visuomotor processing, near targets are typically mislocalized, Medendorp et al. (2003) hypothesized that the shortage of memory vergence for near targets in the absence of motion reflected the mislocalization of the distance of the flashed target.

However, as illustrated here (Fig. 4), memory vergence typically continues to increase throughout the memory period. In contrast, the dynamics of visually guided vergence are typically faster (Fig. 4*B*; see also Maxwell and King 1992; Zee et al. 1992). Thus at least some of the memory vergence errors for the stationary task might stem from the fact that vergence eye movements, typically requiring a closed-loop control system (Collewijn and Erkelens 1990; Horng et al. 1998; Leigh and Zee 1999; Mays and Gamlin 1995), were performed open-loop (i.e., in complete darkness, in the absence of visual feedback) during the spatial memory tasks.

Inherent property or context-specific adaptation?

An important issue to consider is whether the properties of memory-guided saccades during translation described here truly represent a natural state of the system or whether the ability for a distance-dependent compensation for translational/rotational movements arises as a result of extensive behavioral training. Specifically, unlike human subjects who can be asked to perform this task without visual feedback (i.e., memory target being turned on at trial end), monkeys must be extensively trained for several months to learn to perform memory saccades. However, the saccadic system is extremely plastic, with a great ability for "context-specific" adaptation, in which saccadic responses are trained to maintain different values according to some additional input, such as vertical gaze angle or gravitational information (Shelhamer and Clendaniel 2002).

Thus it might seem plausible that the saccadic system could be adaptively trained to exhibit exactly the functionality described here, even if the scaling of response magnitude with target distance were not visually appropriate, using target distance and the nature of provided motion as "contextual" inputs to modify the saccadic response. We have tried to address whether the animals performed an on-line sensorimotor transformation, rather than an arbitrary stimulus-response mapping, by interspersing multiple motion amplitudes within experimental sessions in which no behavioral window was imposed on the memory eye movement. Once animals were trained to perform these tasks, their ability to generalize to different amplitudes, target distances, and convergence/divergence movements suggests that this scaling by target distance might indeed be an inherent property, perhaps having evolved because of a global contextually specific adaptation that has come about simply because of the natural geometry of motion parallax.

Yet, it is important to point out that only experiments with human subjects who are asked to perform these tasks in the absence of visual feedback could provide an unequivocal answer to this question. Interestingly, humans can accurately update the goal of a saccadic eye movement during intervening passive roll head and body rotations only when the movement involves a change in spatial orientation relative to gravity, but not when the rotation occurs in the supine position (Klier et al. 2005). Israel et al. (1999) also reported that humans could perform accurate memory-guided saccades for yaw rotation only after a short period of training in the presence of visual feedback. These results could be interpreted to suggest that, at least for rotational updating, gravitational cues are critical for defining an allocentric (world-fixed) frame of reference. Whether an allocentric reference frame can be unequivocally defined during translation without visual feedback has yet to be tested with future human experiments.

Origin of extraretinal signal: a common target distance scaling of memory saccades and the vestibuloocular reflex?

Estimation of the memory-guided eye movement goal requires both retinal information about the spatial location of the flash and extraretinal information about the nature (rotation vs. translation), direction, and amplitude of the intervening head and body movement. What is the source of such extraretinal information? Unlike the active movements used in the study by Medendorp et al. (2003), extraretinal information in our experiments can arise neither from self-generated cues nor from an efference copy of the motor command. Thus the passive head and body displacements used here leave the vestibular system as the most likely sensory source for motion-related information.

A role of vestibular information in spatial perception has been demonstrated for path integration. Following a passive body displacement, human subjects are able to reproduce the amplitude of the displacement with good accuracy (Berthoz et al. 1995; Israel et al. 1995, 1997; Siegler et al. 2000). The traveled distance could be obtained through time integration of the velocity and acceleration information and stored in spatial memory (Berthoz et al. 1995; Israel and Berthoz 1989; Israel et al. 1997). The results of this study suggest that vestibular information can also interact with visual information to update the goal of memory-guided eye movements.

Scaling by viewing distance has been studied extensively during the TVOR. Similar to the findings of the present study (Fig. 13), the amplitude of compensatory eye movements during translation scales less than expected based on geometry (Angelaki et al. 2000; Schwarz and Miles 1991; Telford et al. 1997; Wei and Angelaki 2004; Wei et al. 2003). The fact that the memory-guided saccade amplitude errors described here are qualitatively similar to those characterizing the amplitude of compensatory eye movements during lateral motion raises the possibility that the two might have a common origin.

Viewing distance–dependent scaling in the TVOR arises primarily through a vergence scaling of the responses of certain premotor neuron groups in the prepositus hypoglossi and vestibular nuclei, known as the Burst-Tonic and Eye-Head cells (Chen-Huang and McCrea 1999; Meng and Angelaki 2003). Although the origin of the signals needed to update the goal of the memory-saccadic eye movements during motion tasks is unknown, it is likely that the necessary extraretinal signals originate from vestibular centers in the brain stem (and/or cerebellum). Under the assumption that visuospatial updating occurs in the visuomotor cortex (Andersen et al. 1997; Goldberg and Bruce 1990), there exist at least two possible pathways by which vestibular signals can reach these areas. The first pathway involves vestibular projections through the ventrolateral thalamus to the so-called parieto-insular vestibular cortex (PIVC) (Grusser et al. 1990a,b), an area that is bidirectionally interconnected with the frontal eye fields (Guldin et al. 1992; Huerta et al. 1987). Because no interconnection was found between frontal oculomotor areas and any of the other vestibular cortical areas (Guldin et al. 1992), it has been suggested that PIVC provides the necessary vestibular signals for vestibular memory-contingent saccades (Berthoz 1997).

Alternatively, the vestibular signals needed for visuospatial updating could follow a route similar to that of other extraretinal signals, i.e., through projections to the paralamellar mediodorsal and intralaminar nuclei of the thalamus (Sommer and Wurtz 2002). These thalamic areas receive projections from the prepositus and vestibular nuclei (Asanuma et al. 1983; Lang et al. 1979; Warren et al. 2003) and have widespread projections to both the frontal and parietal cortexes (Huerta and Kaas 1990; Huerta et al. 1986; Kaufman and Rosenquist 1985; Shook et al. 1990, 1991).

We propose that a similar viewing distance–dependent vestibular signal to that used in the TVOR, perhaps in the form of an efference copy of the suppressed oculomotor drive, is used as an extraretinal compensation for the geometrical consequences of motion parallax by scaling both memory saccades and reflexive eye movements during subject motion through space. Such signals might then be used to completely update the cortical representation of space during either passive or active motions. It is important that future studies address the origins and pathways of extraretinal signals to the sensorimotor centers in the cortex and their involvement in reconstructing a neural map of objects in the environment during movement.

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