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Human Visuospatial Updating After Noncommutative Rotations

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Klier EM, Angelaki DE, Hess BJ. Human visuospatial updating after noncommutative rotations. *J Neurophysiol* 98: 537–541, 2007; First published April 18, 2007; doi:10.1152/jn.01229.2006. As we move our bodies in space, we often undergo head and body rotations about different axes—yaw, pitch, and roll. The order in which we rotate about these axes is an important factor in determining the final position of our bodies in space because rotations, unlike translations, do not commute. Does our brain keep track of the noncommutativity of rotations when computing changes in head and body orientation and then use this information when planning subsequent motor commands? We used a visuospatial updating task to investigate whether saccades to remembered visual targets are accurate after intervening, whole-body rotational sequences. The sequences were reversed, either yaw then roll or roll then yaw, such that the final required eye movements to reach the same space-fixed target were different in each case. While each subject performed consistently irrespective of target location and rotational combination, we found great intersubject variability in their capacity to update. The distance between the noncommutative endpoints was, on average, half of that predicted by perfect noncommutativity. Nevertheless, most subjects did make eye movements to distinct final endpoint locations and not to one unique location in space as predicted by a commutative model. In addition, their noncommutative performance significantly improved when their less than ideal updating performance was taken into account. Thus the brain can produce movements that are consistent with the processing of noncommutative rotations, although it is often poor in using internal estimates of rotation for updating.

INTRODUCTION

The ability to accurately remember the spatial location of an object despite intervening movements of the observer is referred to as visuospatial updating and has been studied extensively (Baker et al. 2003; Blouin et al. 1995a,b, 1998; Herter and Guitton 1998; Israel et al. 1999; Li and Angelaki 2005; Medendorp et al. 2003; Schlag et al. 1990; Van Pelt et al. 2005). Hallett and Lightstone (1976) were the first to show that humans can make accurate saccades to the remembered location of a briefly flashed target after eye movements that dissociated the retinal location of the flash from the required motor command for the eyes. Thus the amplitude and direction of these intervening eye movements are taken into account when planning the next movement. But real life movements typically also involve rotations of the head and body that are largely detected by the semicircular canals of the vestibular system. Israel and colleagues went on to determine that we are relatively accurate at estimating passive pitch and yaw movements of our bodies in space (Israel et al. 1993, 1995; Ivanenko et al. 1997); however, errors were found when subjects at-

tempted to use these estimates of perceived yaw rotation for visuospatial updating (Blouin et al. 1995a,b, 1998; Klier et al. 2006).

More recently, Medendorp et al. (2002) showed that we can take actively generated roll head movements into account for updating, whereas Klier et al. (2005) showed that this ability is still maintained during updating for passive rotations. These studies have supported the hypothesis that the brain utilizes a three-dimensional, noncommutative controller [i.e., the brain takes into account the fact that the order of rotations is important in determining final orientation (Tweed and Vilis 1987)] because updating for torsion requires more complex computations than a simple two-dimensional vector subtraction model can provide (Medendorp et al. 2002).

However, whether human visuospatial updating relies on noncommutative computations has not been studied conclusively because all these previous studies have only tested rotations about one of the cardinal axes (either pure roll, yaw, or pitch). The way to address the issue of noncommutativity is by asking if subjects can update after rotations about two body-fixed axes while alternating their temporal sequence (i.e., rotation about axis **a** followed by rotation about axis **b**, and, conversely, rotation about axis **b** followed by rotation about axis **a** will lead to two different final orientations in space). In fact, because our eyes, head, arms, and torso rotate (as well as translate) about many axes in seemingly random order, taking noncommutativity into account by the underlying neural circuits is critical for accurate visuospatial updating.

But whether the brain actually takes noncommutativity into account in general has been an extremely controversial topic (support for noncommutativity: Crawford and Guitton 1997; Smith and Crawford 1998, 2001; Tweed 1997; Tweed et al. 1994; support for commutativity: Demer et al. 2000; Quaia and Optican 1998; Raphan 1998; Schnabolk and Raphan 1994; Straumann et al. 1995). For example, the vestibulo-ocular reflex can compute the correct noncommutative position signals necessary to hold the eyes steady during whole-body rotations about two axes in different orders (Tweed et al. 1999). In contrast, others have argued that commutative controllers produce good enough approximations using much simpler computations like vector subtraction (Medendorp et al. 2002; Schnabolk and Raphan 1994; Quaia and Optican 1998).

We combined the issues of updating and noncommutativity to determine if human subjects can accurately compute the spatial location of a target after two consecutive rotations (i.e., first roll then yaw then yaw then roll). The reasoning behind this noncommutative updating study arises from the following

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logic. 1) It has been shown that subjects can update the spatial location of a briefly flashed target after a single, intervening body rotation. 2) However, rotations are inherently noncommutative (rotation A followed by rotation B does not result in the same final orientation as rotation B followed by rotation A). 3) Thus can subjects correctly localize a briefly flashed target after a sequence of two intervening body rotations when the order of rotations is reversed? This question is not trivial as the subject's final orientations will be different depending on the order of rotations and thus different movements to the same remembered space-fixed target location will be required. If subjects do this task accurately, this would imply that the brain can produce the correct noncommutative endpoints required to update the remembered target locations.

METHODS

Subjects

Six subjects (4 female and 2 male) ranging in age from 27 to 37 yr old were recruited to participate in the experiment. All but one (*EK*) were completely naïve to the purpose of the experiment and none had any known neuromuscular or neurological damage. All subjects gave informed consent to the experimental protocol that was approved by the Ethics Committee of the Canton of Zurich, Switzerland.

Measuring three-dimensional eye position

Three-dimensional eye positions were measured using the magnetic search coil technique and three-dimensional Skalar search coils (Skalar Instruments, Delft, The Netherlands). The magnetic field system consisted of three mutually orthogonal magnetic fields, generated by a cubic frame with side lengths of 0.5 m, operating at frequencies of 80, 96, and 120 Hz. Three-dimensional eye position was calibrated by using an algorithm that simultaneously determined the orientation of the coil on the eye and offset voltages based on nine target fixations in close-to-primary and secondary gaze positions (Klier et al. 2005).

Experimental protocol

Subjects sat on a chair that was mounted on a three-dimensional turntable (Acutronic, Bubikon, Switzerland) capable of rotating subjects in both yaw and roll. The three axes of rotations used for this experiment were an inner yaw axis centered on the longitudinal axis of the subject, a roll axis centered on the naso-occipital axis of the head, and an outer yaw axis centered on the body as the inner yaw axis. In this way, a yaw axis (inner) could be nested within a roll axis (for the roll-then-yaw sequence), and conversely, a roll axis could be nested within a yaw axis (outer; for the yaw-then-roll sequence). As a control, in addition to these consecutive rotational sequences, we also ran the experiment with rotations about both axes occurring concurrently. This resulted in single axis rotations whose components (yaw and roll) were differentially nested as stated in the preceding text, and the endpoints of which were the same as those in the consecutive conditions. For all these rotations, constant accelerations/decelerations were used, resulting in triangular velocity profiles (i.e., velocity increased linearly to a peak and then decreased linearly back to 0; see Fig. 1).

The subjects' bodies were fixed to the chair by three restraining methods. First, aviation safety belts secured the upper and lower torso to the chair. Second, evacuation pillows filled the empty spaces under the arms and around the neck. Finally, a malleable thermoplastic mask was molded to each subject's face and fastened to the chair behind the subject's head. This mask kept the subject's head fixed relative to the rest of their body so that movement of the chair caused the head and

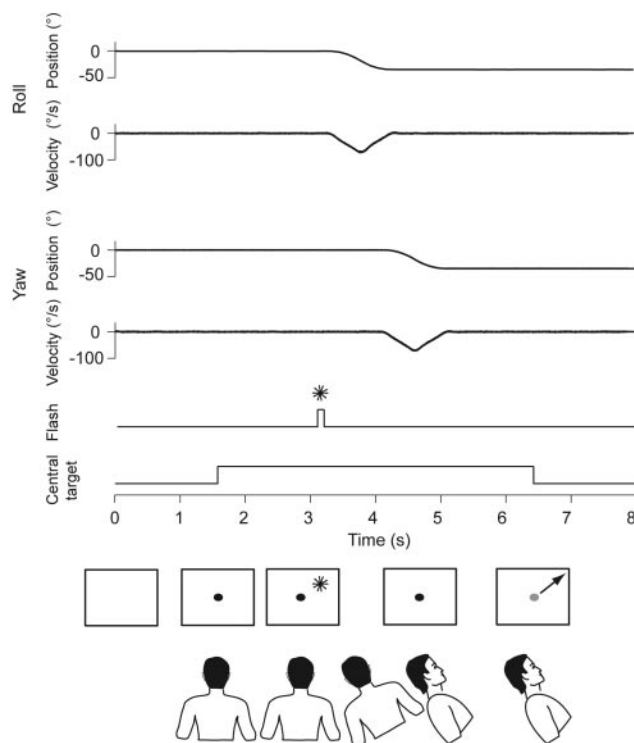


FIG. 1. An example of a typical roll-then-yaw trial. The position (rows 1 and 3) and velocity (rows 2 and 4) profiles of the chair's rotation about the 2 body-fixed axes are plotted versus time for both roll (rows 1 and 2) and yaw (rows 3 and 4) components. The central target remained illuminated throughout the peripheral flash and two rotational sequence. The subject was cued to make a saccade to the remembered location of the peripheral flash when the central target was extinguished.

body to move as one unit (i.e., the head was on the rotation axis). Visual targets were produced by a computer-controlled laser and projected onto a spherical projection screen located 1.45 m in front of the subject (the screen provided a visual angle of 100°).

In complete darkness, each trial began with the subject fixating a central target [light-emitting diode (LED); Fig. 1]. After 1.5 s, a peripheral target was briefly flashed for 100 ms [the peripheral target was generated by a laser the position of which was determined by horizontal and vertical galvanometers (General Scanning)]. The peripheral target was presented at an eccentricity of 18° and an angle of 30, 45, or 60° from the horizontal in each of the four quadrants (the 30° targets were those closest to the abscissa, whereas the 60° targets were closest to the ordinate). The subjects were instructed to keep fixating the central target, but remember the location of the flash. Immediately after the flash, the subjects were taken through one of the following rotation protocols: rotation protocol 1, 35° roll followed by 35° yaw (inner axis); rotation protocol 2, 35° yaw (outer axis) followed by 35° roll.

To keep the final positions of the space-fixed targets within the subject's oculomotor range, specific directional combinations were used depending on the quadrant of the flashed target. For example, if the peripheral target was flashed in the first quadrant (i.e., up and to the right of the central target), then the roll-then-yaw sequence consisted of a counterclockwise rotation followed by a rightward rotation and the yaw-then-roll sequence consisted of a rightward rotation followed by counterclockwise rotation. Using the same rationale, targets in the second quadrant were paired with clockwise and leftward rotations, targets in the third quadrant were paired with counterclockwise and leftward rotation, and targets in the fourth quadrant were paired with clockwise and rightward rotations. The time between the end of the first rotation and the start of the second rotations varied somewhat due to factors such as the weight of each

subject, however, across all trials, the maximum time difference recorded between rotations was 300 ms.

In addition to these rotations, in which movement about one axis finished before movement about the second axis began, we also repeated these protocols by rotating about both axes simultaneously. Doing this with the inner yaw axis nested inside the roll axis resulted in a final orientation coincident with the roll-then-yaw protocol, whereas nesting the roll axis inside the outer yaw axis led to the same final orientation as the yaw-then-roll protocol. These concurrent rotations were used as controls to show that differences inherent to how the axes were nested, rather than temporal timing, were the relevant factors in performance. Each trial consisting of one rotation protocol and one target was randomly repeated four times, and the consecutive and concurrent trials were also intermixed randomly.

During each trial the subjects were required to maintain their fixation on the central target, which remained illuminated and moved along with the subject (i.e., head-fixed; (adherence to this requirement was checked off-line by the experimenters and violations greater than 5° were eliminated from further analysis). On completing the rotation sequence, the central target remained illuminated for an additional 1.5 s. Extinguishing the central target cued the subjects to make a single saccade, as accurately as possible, to the remembered, space-fixed location of the flash. The true location of the flashed target never re-appeared so subjects did not receive feedback about their accuracy and thus no learning could take place. On completing the experiment, each subject was asked several questions about their perception of the experiment and their performance. No subjects reported feeling any postrotatory motion (and subsequently no postrotatory nystagmus was observed off-line), and all thought they had accurately localized the remembered target locations.

Data analysis

Raw data from each subject's right eye, sampled at 833 Hz, was first converted into rotation vectors, which indicate the horizontal, vertical, and torsional positions of the eye. These positions were subsequently transformed into eye velocity by taking the derivative of eye position ($dE/dt =$ where E is 3-dimensional eye position). Finally, angular eye velocity (Ω) was computed from the previous two values by the equation $\Omega = 2 (dE/dt + E \times dE/dt)/(1 + |E|^2)$ (where \times designs the cross vector product) (Hepp 1990). All saccade trajectories to the remembered target locations were automatically selected using the following criteria: the start of a saccade was selected when the square root of the sum of squares of the horizontal, vertical and torsional angular velocities exceeded $10^\circ/s$. The end of a saccade occurred when the same value decreased $<10^\circ/s$. These data, along with the actual locations of the targets in space, allowed us to plot saccade trajectories and endpoints, compute polar and Cartesian errors, and conduct statistical analyses (t -test and ANOVAs) on our data.

Updating ratios

The accuracy of the subjects' saccades relative to the location of the targets was quantified to determine how well subjects took their intervening body movements into account when making saccades to the remembered location of the flashed target. Three measures were used for this analysis: the space-fixed location of the target (assuming perfect updating for intervening body motion), the head-fixed location of the target (assuming no updating for body motion), and the subject's final gaze position (i.e., the memory saccade endpoint). The errors were expressed in either Cartesian (x,y) or Polar (r,ρ) coordinates. For yaw rotations, the target locations must be updated along the horizontal dimension (x), whereas for roll rotations, the horizontal and vertical directions (i.e., angle, ρ) of the target locations must be updated. As a result, data in our combined rotation protocols are

summarized in terms of both the horizontal (x) as well as the angular (ρ) dimensions.

The horizontal and angular updating ratios were computed as follows: first, we measured the horizontal (x_{actual}) and angular (ρ_{actual}) distance between the subject's gaze endpoint and the head-fixed location of the flash. Second, we computed the total distance the subject had rotated by taking the horizontal (x_{ideal}) and angular (ρ_{ideal}) distance between the space- and head-fixed locations of the target. Finally, we divided $x_{\text{actual}}/x_{\text{ideal}}$ and $\rho_{\text{actual}}/\rho_{\text{ideal}}$ to obtain the horizontal updating ratio (UR x) and the angular updating ratio (UR ρ), respectively, representing how much of the rotation the subjects compensated for when executing their saccades (see Fig. 2A in Klier et al. 2005). A value of 1 indicates perfect updating for the intervening rotation, whereas a value of 0 indicates no updating (i.e., the subject made a saccade to the head-fixed location of the target). Values between 0 and 1 indicate partial updating, values >1 represent saccades that overcompensated for the intervening rotation by missing the actual space-fixed target location in a direction opposite to that of the head-fixed target location, and negative values result from saccades that miss the head-fixed target in a direction opposite to that of the space-fixed location of the target.

Noncommutative ratio

Noncommutative rotations from one starting position necessarily lead to different final end positions. The distance between these two final noncommutative positions can easily be calculated as follows

$$D_{\text{NC}} = \sqrt{(x_{\text{RY}} - x_{\text{YR}})^2 + (y_{\text{RY}} - y_{\text{YR}})^2}$$

Where D_{NC} is the distance between noncommutative endpoints, x_{RY} is the x component of the yaw-then-roll rotation combination, and x_{YR} is the x component of the roll-then-yaw rotation combination (the subscript letters should be read from right to left as indicated by standard mathematical notation). y is the y component of these endpoints. In contrast, the commutative endpoints must always lie in the exact same location (i.e., the order of rotations does not matter—the final endpoints are identical). Thus using the equation above to calculate the distance between two commutative endpoints (D_{C}) will always produce values of 0.

The preceding formula can also be used on the subjects' actual endpoints, and the distance between the endpoints in the roll-then-yaw versus yaw-then-roll conditions can be calculated (D_{actual}). With these

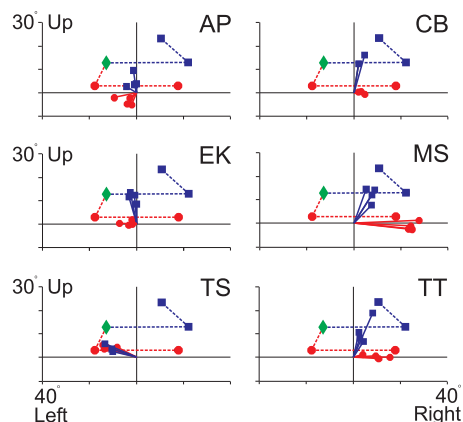


FIG. 2. Noncommutative predictions for perfect updating and actual performances for consecutive rotations. The predicted endpoints of the space-fixed target (green diamond) after yaw-then-roll (with roll-nested-in-yaw; blue square) vs. roll-then-yaw (with yaw-nested-in-roll; red circle) rotation protocols are shown connected by dashed lines. The 6 subjects' endpoints are indicated by corresponding symbols (blue square and red circle) connected to the origin by solid lines. All the endpoints are the tips of 3-dimensional rotation vectors in space coordinates.

values, we can compute a noncommutative ratio (NCR), where $NCR = D_{actual}/D_{NC}$. If the subjects perform accurate saccades that take their eyes to the correct noncommutative locations, then the ratio of the subjects' distance (D_{actual}) divided by the theoretical noncommutative distance (D_{NC}) should yield a value of 1. A value of 0 would indicate that the subjects moved their eyes to the same location in space irrespective of the order of the rotational axes used, and this would support a commutative model.

This ratio is a good measure of whether subjects behaved in a commutative or noncommutative manner because it evaluates whether the eye movements to the roll-then-yaw versus yaw-then-roll targets either remained the same or diverged in different directions. And it is this directional difference [Fig. 2 – the final roll-then-yaw endpoint (blue square) is located above the original target flash (diamond)], whereas the final yaw-then-roll endpoint (red circle) is located below the original target flash (diamond)] that is predicted by the cross-product inherent in the noncommutative mathematics used when combining two rotations to compute the two unique final orientations (Goldstein 1980). Note that both the updating and noncommutative ratios were computed in space coordinates.

The NCR computed with the raw data [which uses the subject's actual endpoints (numerator) and the theoretical noncommutative endpoints (denominator) as shown in Fig. 2], includes errors attributable to both the subject's less-than-ideal updating ability and the subject's noncommutative performance. To eliminate the errors attributable to updating ability, we recomputed new theoretical endpoints (i.e., a new denominator— D_{NC}^*) and subsequently a new NCR (referred to as NCR^*) by taking the subjects' performances in the roll-only (Klier et al. 2005) and yaw-only (Klier et al. 2006) experiments as "perfect" updating performances. Thus the new NCR^* is a better measure of the subject's noncommutative ability alone. This procedure was conducted in the following way.

Starting with the yaw- and roll-only trials, we took each flashed target location, $T = (x_T \ y_T \ z_T)$ and each memory saccade endpoint, $T' = (x_{T'} \ y_{T'} \ z_{T'})$ (where x, y, z are the Cartesian coordinates along the naso-occipital, interaural, and vertical head axes), and we computed the brain's estimate of angular change in target direction due to the rotation of the observer. In the yaw paradigm, this rotation angle (ϑ) follows from the dot product of these two vectors, each projected onto the yaw plane ($z_T = z_{T'} = 0$)

$$\vartheta(T, T') = \cos^{-1}((x_T x_{T'} + y_T y_{T'}) / \sqrt{(x_T^2 + y_T^2)(x_{T'}^2 + y_{T'}^2)})$$

Thus for the underlying yaw updating we write $T \rightarrow T' = R(\vartheta)T$, where $R(\vartheta)$ describes the estimated horizontal rotation of the visual direction of the flashed space-fixed target T relative to the subject through the angle ϑ . In an analogous manner, the rotation angle (ρ) in the roll paradigm is obtained from the dot product of flashed target and memory saccade vector, each projected on the roll plane ($x_T = x_{T'} = 0$)

$$\rho(T, T') = \cos^{-1}((y_T y_{T'} + z_T z_{T'}) / \sqrt{(y_T^2 + z_T^2)(y_{T'}^2 + z_{T'}^2)})$$

Using this angle, we describe the roll updating of the visual direction of the flashed target T relative to the subject by a rotation $R(\rho)$ about the naso-occipital axis through the angle ρ .

These yaw- and roll-only rotations represent eye movements that compensated for less than the whole 35° rotations (on average, subjects accounted for 72% of the yaw movement and 92% of the roll movement – see Table 1). We then used these values as each subject's perfect updating behavior (e.g., on average, the subjects updated perfectly for a 25.2° yaw movement and a 32.2° roll movement based on the percentages given in the preceding text).

To predict the noncommutativity based on the performance in these yaw- and roll-only rotation paradigms, we write the overall relative change in target orientation by applying the yaw and the roll rotations in two orders, $T \rightarrow T_{RY}' = R_\rho R_\vartheta T$ and $T \rightarrow T_{YR}' = R_\vartheta R_\rho T$, on the flashed target location T (for each single experimental trial). Using the experimentally determined ρ and ϑ values from the previously performed yaw- and roll-only paradigms, we estimated new expected noncommutative updating performance after a yaw-then-roll and roll-then-yaw rotations by again computing the average distance between the new theoretical endpoints (D_{NC}^*) based on the coordinates of T_{RY}' and T_{YR}' , and subsequently computing NCR^* .

RESULTS

After two noncommutative rotations, the subject's final orientations in the yaw-then-roll and roll-then-yaw sequences were different from one another and thus required different saccade trajectories to accurately reach the remembered target locations. The predictions of the 35° rotation endpoints are given in Fig. 2 (dashed lines). The illustrated example is of a target that was initially shown at 45° in the second quadrant (green diamond). For the yaw-then-roll rotation sequence (blue square), the movement of the target relative to the subject is shown by blue dashed lines connecting the diamond with the blue squares: first a yaw-only rotation, then a roll-only rotation. Although the target itself was space-fixed and did not move (i.e., only the subject was rotated), here for illustrative purposes, we show how the target moved relative to the subject (the subject's gaze is fixed on the origin throughout the rotation). The roll-then-yaw rotation sequence (circle) is shown in red. The theoretical endpoints of these two different rotation protocols clearly end up in different spatial locations.

The subjects' actual saccadic endpoints are shown by the corresponding symbols (blue square for yaw-then-roll and red circle for roll-then-yaw), connected to the origin by solid lines. There was clear variability in the subjects' performances.

TABLE 1. Average horizontal updating ratios (URx), angular updating ratios (URρ), and non-commutative ratios (NCR) for all six subjects

Subject	URx (Y only)	URρ (R only)	URx		URρ		NCR	
			Y then R	R then Y	Y then R	R then Y	NCR	NCR*
AP	0.46 ± 0.12	1.16 ± 0.24	0.20 ± 0.22	0.23 ± 0.11	1.35 ± 1.05	1.52 ± 1.14	0.41 ± 0.24	0.91 ± 0.52
CB	0.45 ± 0.06	0.69 ± 0.22	0.58 ± 0.06	0.47 ± 0.09	0.98 ± 0.31	1.04 ± 0.62	0.37 ± 0.14	1.36 ± 0.74
EK	0.66 ± 0.08	0.62 ± 0.18	0.33 ± 0.12	0.29 ± 0.11	1.02 ± 0.63	1.13 ± 0.89	0.39 ± 0.18	0.96 ± 0.48
MS	1.11 ± 0.13	1.24 ± 0.48	0.63 ± 0.14	0.90 ± 0.17	1.06 ± 0.29	1.67 ± 1.25	0.81 ± 0.26	0.66 ± 0.26
TS	0.66 ± 0.09	0.77 ± 0.35	0.01 ± 0.14	0.06 ± 0.10	1.31 ± 1.33	1.34 ± 1.10	0.23 ± 0.15	0.63 ± 0.60
TT	0.92 ± 0.13	1.02 ± 0.15	0.75 ± 0.11	0.67 ± 0.09	1.00 ± 0.15	1.16 ± 0.52	0.67 ± 0.22	0.75 ± 0.30
Average	0.71 ± 0.26	0.92 ± 0.37	0.41 ± 0.30	0.42 ± 0.34	1.13 ± 0.75	1.13 ± 0.95	0.48 ± 0.28	0.88 ± 0.55

Values are means ± SD. Individual data points for each of 12 target locations (i.e., 3 target directions (30°, 60°, 90°) × four quadrants) are illustrated in Figs. 3 and 4B. URx and URρ, horizontal and angular updating ratios, respectively. Y, yaw; R, roll.

Specifically, three subjects seem to have updated quite accurately (*CB*, *MS*, *TT*), whereas the other three did not do as well (*AP*, *EK*, *TS*).

Updating ratio

How well the actual saccade endpoints agreed with the predictions was quantified using an updating ratio (see METHODS). We first computed horizontal (UR_x) and angular (UR_ρ) updating ratios for each subject, for each target location (30, 45, 60°), in all four quadrants. The horizontal ratios (ordinate axis in Fig. 3A) show that the subjects' performances typically fell in between 0 and 1, indicating varying degrees of updating performance across subjects (average UR_x for roll-then-yaw = 0.42 ± 0.34 ; average UR_x for yaw-then-roll = 0.41 ± 0.30). In contrast, the angular ratios (ordinate axis in Fig. 3B) showed more scatter and ranged in values from 0 to 4 [average (UR_ρ) for roll-then-yaw = 1.31 ± 0.95 ; average (UR_ρ) for yaw-then-roll = 1.13 ± 0.75]. Average values for all subjects are shown in Table 1. Across both ratios, however, one can see that there is some clustering of the data points for each subject [different symbols, for example subject *TS* (triangle) who showed relatively poor performance]. Thus each subject had a consistent level of performance, but this level varied across subjects.

We next compared how well subjects could update with combined rotations as compared with single axis rotations that involve only pure yaw or pure roll axes. The data for these single axis conditions were taken from two previous studies (Klier et al., 2005, 2006) that used the same six subjects. Figure 3 compares updating performance for both the UR_x (A, comparing the combined horizontal component with yaw-only rotations) and the UR_ρ (B, comparing the combined directional component with roll-only rotations). In both cases, the data spread along the ordinate [although this is more evident for the angular ratio (ρ)], indicating that there was much more variability in performance for combined than cardinal axes rotations. Again, notice how data from each subject seems to cluster together, pointing to less intrasubject variability and

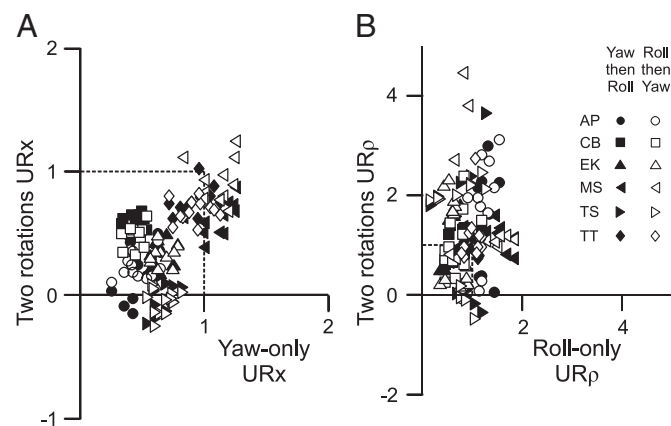


FIG. 3. Comparing double- and single-axis rotations. *A*: horizontal updating ratio (UR_x) is used to compare subjects' performances in the consecutive combined vs. cardinal yaw-only conditions. *B*: angular (i.e., directional) ratio (UR_ρ) is used to compare subjects' performances in the consecutive combined vs. cardinal roll-only conditions. Yaw-then-roll data are illustrated by black symbols and roll-then-yaw data are shown in white. Each subject is represented by a different symbol. A value of 1 indicates perfect updating (dashed lines), whereas a value of 0 indicates no updating. Average values for all subjects are given in Table 1.

more intersubject variability. Average values for all subjects are given in Table 1.

We also compared UR_x and UR_ρ when the rotations were delivered consecutively (i.e., rotation about 1 axis finished before rotation about the 2nd axis began) versus concurrently (i.e., the rotations occurred simultaneously). Regression analyses indicated no differences between subjects' performances in the two conditions, with UR_x of 1.01 (95% confidence interval: [0.74, 1.32]; $r^2 = 0.84$; $P = 0.000$) for roll-then-yaw and 0.79 (95% confidence interval: [0.63, 1.16]; $r^2 = 0.83$; $P = 0.000$) for yaw-then-roll. The UR_ρ were 1.10 (95% confidence interval: [0.94, 1.49]; $r^2 = 0.80$, $P = 0.000$) for roll-then-yaw and 1.10 (95% confidence interval: [0.96, 1.31]; $r^2 = 0.95$, $P = 0.000$) for yaw-then-roll.

Noncommutative ratio

The noncommutative ratio (NCR - see METHODS) was then used to quantify if subjects' saccades landed on two distinct locations (rather than 1 unique location) by measuring the difference in endpoint positions for the two rotational combinations. The absolute average distance between the subjects' yaw-then-roll and roll-then-yaw endpoints was $10.3 \pm 6.0^\circ$, and this value was significantly different from 0 (t -test, $P = 0.000$). But this measure does not indicate how well the subjects performed in comparison to the theoretical distance between yaw-then-roll and roll-then-yaw endpoints [the theoretical average distance across all 3 targets (30, 45, and 60°) was $21.4 \pm 0.4^\circ$]. Thus we computed their respective NCR. Figure 4A plots the NCR, for all six subjects, separately according to the location of the target flash: the 30° targets (white bars), the 45° targets (black bars), 60° targets (gray bars). A value of 1 indicates that the distance between subjects' endpoints in the yaw-then-roll versus roll-then-yaw conditions were the same as those expected from theoretical endpoint distance calculation, whereas a value of 0 indicates that subjects were directing their saccades to the same endpoint location, irrespective of the sequence of the rotational axes (i.e., subjects are using a commutative controller).

The average (\pm SD) values of the NCR were 0.43 ± 0.22 , 0.51 ± 0.19 , and 0.50 ± 0.26 for the 30, 45, and 60° targets, respectively (average NCR values for each subject are shown in Table 1). Although the NCR values shown in Fig. 4A were significantly different from a value of 1 (t -test, $P = 0.000$), they were also different from a value of 0 (t -test, $P = 0.000$). On average, the values were not different from 0.5 (t -test, $P = 0.541$), indicating that subjects were compensating for ~50% of the total distance between the two noncommutative endpoints. A univariate ANOVA indicated no differences in the NCR values across the different target locations [$F(3,20) = 2.354$, $P = 0.103$].

We then compared the updating and noncommutative ratios for each subject (Fig. 4B). On looking at the theoretical predictions in Fig. 2, it becomes clear that most of the change in final target position results from the yaw rotation (i.e., equal rotations of 35° for yaw and roll move the target differentially on a fronto-parallel surface—the change in yaw being greater than the change in roll). For this reason, the UR_x is a better indicator of subject's performance than the UR_ρ , and thus this comparison was made with the UR_x . The regression line (Fig. 4B) had a slope of 1.17 (95% confidence interval: [0.78, 1.85];

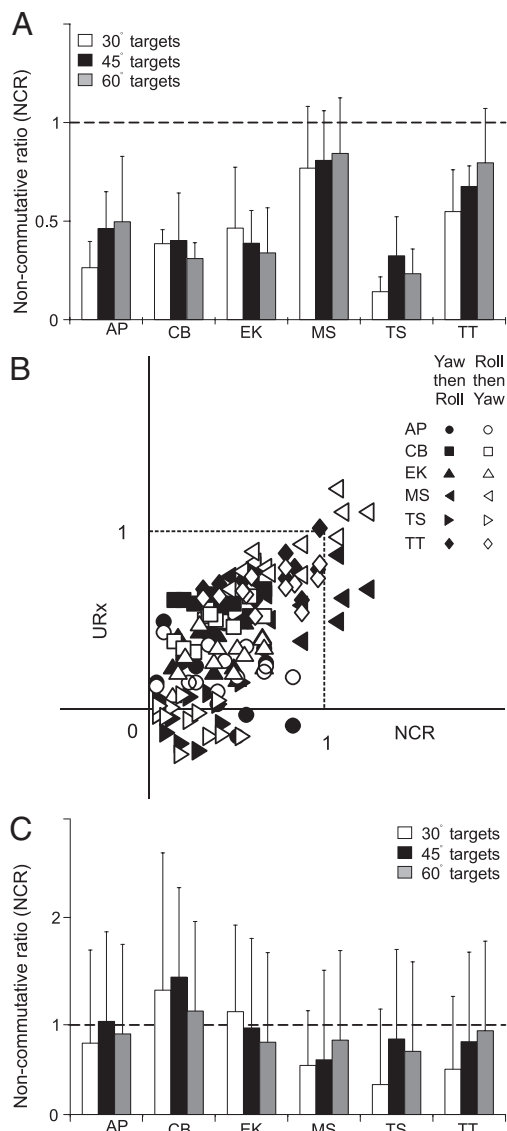


FIG. 4. Noncommutative updating ratio. **A**: noncommutative ratio (NCR, see METHODS) is computed and plotted for all 6 subjects, for each target location. White bar, 30° targets; black bar, 45° targets; gray bar, 60° targets. A value of 1 indicates that the subjects' endpoints were as far apart as predicted by the noncommutative model, whereas a value of 0 indicates that the subjects' endpoints were coincident as would be predicted by a commutative model. **B**: horizontal updating ratio (URx) is compared with the noncommutative ratio (NCR) for yaw-then-roll (black symbols) and roll-then-yaw (white symbols) conditions. Each subject is represented by a different symbol. A value of 1 indicates perfect updating along the ordinate, whereas a value of 1 indicates that subjects' endpoints were directed to different endpoints as predicted by noncommutativity. Average values for all subjects are shown in Table 1. **C**: new NCR* computed after each subject's yaw-only and roll-only updating performance was taken into account. Bars and axes labeled as in **A**.

$r^2 = 0.48$; $P = 0.000$) for yaw then roll and a slope of 1.29 (95% confidence interval: [1.08, 1.63]; $r^2 = 0.73$; $P = 0.000$) for roll then yaw. These near-unity slopes indicate that subjects who exhibited good updating ability were equally good at the noncommutative aspect of the task (e.g., *TT*, diamond, and *MS*, triangle), whereas those who had poor updating ratios had similarly poor noncommutative ratios (e.g., *TS*, triangle, and *AP*, circle).

Because these two ratios are so well correlated, it is possible that the relatively large errors found in both ratios come from an inability to accurately update after passive whole-body rotations. This is evidenced by the fact that subjects update rather poorly during yaw-only rotations (see Klier et al. 2006 and spread of data along abscissa of Fig. 3A). Subjects' systematic (but not variable) errors are lower during updating for roll-only rotations (Klier et al. 2005 and Fig. 3B); however, small errors still occur. Thus we recomputed the theoretical final endpoints (blue square for yaw then roll and red circle for roll then yaw in Fig. 2) by taking into account the subjects' average endpoints in the yaw- and roll-only tasks as perfect performances (see METHODS). For example, if a subject in the 35° yaw-only task had a horizontal updating ratio of 0.5, then we considered it to represent a perfect updating performance for a body rotation of 17.5° (i.e., half the magnitude of the real rotation amplitude). When both yaw- and roll-only performances were taken into account, the overall NCR rose significantly (t -test, $P = 0.000$) from an average of 0.48 ± 0.28 (precorrection) to an average of 0.88 ± 0.55 (postcorrection; Fig. 4C and Table 1).

DISCUSSION

We set out to determine if the brain can contend with the mathematical complexities associated with the noncommutativity of rotations during a visuospatial updating task. We found that some subjects could combine consecutive rotations about two different axes and subsequently compute different motor commands depending on whether the sequence of rotations was yaw then roll or roll then yaw, but others could not. Even for those that could, the computed endpoints were not nearly as disparate as would be predicted by perfect noncommutativity. However, once the subjects' single axis rotation errors were taken into account, the accuracy of their saccade endpoints during consecutive rotations greatly improved. Thus the brain can generate movements that are consistent with the noncommutativity of rotations, but it is somewhat poor at updating after passive whole-body rotations in general.

Updating variability

Half of our subjects (3/6) were able to update quite well, two had saccade endpoints that landed in between the head-fixed and space-fixed locations of the target [including the 1 non-naïve subject (*EK*)], and one (*TS*) did not show any updating. Differences in performance were unlikely attributable to differences in experience with such tasks or to difficulties in understanding the nature of the task because all six had previously been subjects in this same apparatus on numerous occasions and all six had shown an ability to update in two previous experiments (see Fig. 3) (data for single axes from Klier et al. 2005, 2006). There, average URx was measured to be 0.71 ± 0.26 for the yaw-only condition and average UR ρ was 0.92 ± 0.37 for roll-only condition, indicating better ability to update in roll than in yaw (Klier et al. 2006). In contrast, the average URx was much lower for the two consecutive rotations in this study: 0.41 ± 0.30 for yaw then roll and 0.43 ± 0.34 for roll then yaw.

One difference between single- and double-rotation trials is that the time course of the double rotation updating task takes

approximately twice as long as the single rotation task (each 35° rotation about each axis took ~2 s). Thus subjects had to keep the memorized location of the target in working memory for an extended period of time in the current study. One may speculate that since the memory of a previously viewed target has been shown to decay over time (White et al. 1994), then this extended time interval may have contributed to some of the additional error seen in the current experiment. However, this was not the case because updating performances in the consecutive and concurrent rotation trials were identical.

One possible explanation for the poorer performance observed when updating after two rotations about two different axes instead of just one is the idea of reference frames. Updating after yaw rotations has shown better performance when the targets are memorized in an egocentric (body-fixed) frame of reference (Baker et al. 2003), but Van Pelt et al. (2005) found that roll updating operates in an allocentric reference frame. It is not known if our double-rotation task forces the brain to choose one unique reference frame in which to compute final eye positions in space, or if an intermediate frame is employed. In either case, transforming stored memories from one frame to another may have led to the larger observed errors (i.e., errors that were larger than in the yaw- and roll-only conditions).

Overall performance in updating may have also shown improvement if the rotations were self-generated rather than passive. Such a difference has been shown for saccades with roll-only rotations [active (Mendendorp et al. 2002) vs. passive (Klier et al. 2005)] and for pointing accuracy after self-generated yaw rotations (Blouin et al. 1995c, 1998). Even passive head-on-body rotations can improve updating accuracy (Mergner et al. 1988) likely due to the processing of cervical afferent signals. Finally, practice and learning have been shown to play important roles in our ability to perform updating tasks (Baker et al. 2003; Israel et al. 1999; Li et al. 2005), something our subjects were not permitted.

Noncommutativity

Despite errors in updating, Fig. 4B indicates that subjects who had updating ratios close to 1 had equally good noncommutative ratios, whereas those with updating ratios close to 0 had equally poor noncommutative ratios. This correlation suggests that poor updating performance may have been the reason behind the relatively small noncommutative ratios (i.e., why subjects compensated for only half of the total noncommutative distance between endpoints). Indeed, by taking the subjects' performances in the yaw- and roll-only experiments into account, the non-commutative ratio significantly improved from 0.48 to 0.88.

Tweed and colleagues were the first to bring to light the idea that the brain must contend with the noncommutativity of rotations (Tweed 1997; Tweed and Vilis 1987), and they were the first to test if the oculomotor system takes these properties into account (Tweed et al. 1999). In their study, subjects looked straight ahead as their bodies were rotated in a sequence of two rotations: first yaw then roll, then roll then yaw. The subjects' final eye positions in the two conditions were measured, and it was found that these final orientations differed depending on the order of rotations. Unlike in this passive study, in the present study, we show that subjects can generate

movements consistent with the noncommutativity of rotations even with the location of memorized (i.e., nonvisualized) targets. Thus the brain can actively combine a memorized, two-dimensional retinal error vector with a series of three-dimensional rotational vectors to produce distinct movement endpoints.

The only other three-dimensional behavioral study to examine noncommutativity in an updating task found small errors during double-step saccades to remembered visual targets that were much smaller than those predicted by a commutative model (Smith and Crawford 2001). This was a purely visual-saccade task in contrast to our visual-vestibular-saccade paradigm and thus updating mechanisms in the brain appear to be capable of correctly processing three-dimensional signals both for the saccadic system as well as for passive vestibular inputs.

Noncommutativity versus gravity

Although our results are consistent with the brain performing noncommutative mathematical operations, our study cannot confirm how such computations are actually being made by the underlying neural circuitry. For example, it is possible that our subjects could have made use of gravity-related (e.g., otoliths) signals for updating (and not solely canal cues). In such a scheme, subjects could compare gravity cues in the initial upright positions with the differential gravity signals in the two final orientations and then use the differences to generate the necessary eye movements. These gravity cues along with a commutative neural controller could give rise to the same noncommutative endpoints. However, although we and others have shown that gravity may play some role in updating about the roll axis (Klier et al. 2005; Van Pelt et al. 2005), we recently showed that gravity does not aid in updating about the yaw axis, even when the body's yaw axis and the gravity vector are not aligned (Klier et al. 2006). Thus in the current experiment, a static otolith-derived gravity cue was not likely the main factor in generating accurate noncommutative endpoints. In addition, a more recent noncommutative study on whole-body, self-motion perception, that controlled for gravity cues (i.e., the initial and final body orientations relative to gravity were the same irrespective of the order of rotations), has shown that subjects are accurate at reporting their perceived orientation in space after two noncommutative rotations (Glasauer and Brandt 2007).

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