Non-commutative updating of perceived self-orientation
in three dimensions

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Running head: Updating self-orientation

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Abstract

After whole body rotations around an earth-vertical axis in darkness, subjects can indicate their orientation in space with respect to their initial orientation reasonably well. This is possible, because the brain is able to mathematically integrate self-velocity information provided by the vestibular system to obtain self-orientation. This process is called path integration. For rotations around multiple axes, however, computations are more demanding to accurately update self-orientation with respect to space. In such a case, simple integration is no longer sufficient due to the non-commutativity of rotations. We investigated whether such updating is possible after three-dimensional whole body rotations, and whether the non-commutativity of three-dimensional rotations is taken into account. The ability of ten subjects to indicate their spatial orientation in the earth-horizontal plane was tested after different rotational paths from upright to supine positions. Initial and final orientation of the subjects were the same in all cases, but the paths taken were different, and so were the angular velocities sensed by the vestibular system. The results show that seven of the ten subjects could consistently indicate their final orientation within the earth-horizontal plane. Thus, perceived final orientation was independent of the path taken, i.e., the non-commutativity of rotations was taken into account.
Introduction

Vestibular input signaling angular self-velocity is sufficient to notice changes of self-orientation in space (Mach 1875). Previous experiments have shown that subjects can estimate their orientation after short whole body rotations around the earth vertical axis in complete darkness (e.g., Guedry 1974; Mergner et al. 1991; Israel et al. 1995; Mittelstaedt & Mittelstaedt 1997; Marlinsky 1999; Jürgens et al. 1999). During this task, the only available information about movement in space is the angular self-velocity sensed by the vestibular system. Consequently, estimating self-orientation in space requires that the angular velocity cue from the vestibular system is mathematically integrated to yield self-orientation. This process is part of an ability called path integration (Mittelstaedt & Mittelstaedt 1980) or inertial idiothesis (Mittelstaedt & Glasauer 1991). Path integration provides means to update knowledge of one’s spatial position and orientation (Klatzky et al. 1998).

If, however, the rotation involves more than a single axis, e.g., first a rotation around the subject’s yaw axis and subsequently a rotation around the pitch axis, a simple integration of angular velocity no longer suffices due to the kinematics of three-dimensional rotations. Instead, to accurately compute self-orientation in space from angular velocity signals, the instantaneous orientation has to be taken into account, since rotations do not commute. In other words, the final orientation depends on the order of the applied rotations.

It has been shown that the brain accounts for the non-commutativity of rotations when the vestibulo-ocular reflex stabilizes gaze during whole body rotations (Tweed et al. 1999), or during the remapping of visual targets during eye or head movements (Smith & Crawford 2001; Medendorp et al. 2002; Crawford et al. 2004). It is not known at present whether this also holds for the updating of self-orientation. A straight-forward way to test this hypothesis would be to submit subjects to the same passive whole body rotations, but in different order, thus yielding different final orientations. This approach has been used before for the vestibulo-ocular reflex (Tweed et al. 1999).
Here we used an alternative approach which is equally well-suited to test whether non-commutativity is taken into account by the updating process: if different rotations starting at the same initial orientation and yielding the same final orientation are applied, any commutative operation should result in differences in perceived final self-orientation. This approach can also be regarded as a test if estimation of self-orientation is path-independent. Appendix 1 shows that our approach can indeed be used as an equivalent test of whether the path-integration process\(^1\) was aware of the non-commutativity of rotations.

On earth, rotations around more than one axis necessarily involve changes with respect to gravity. The straightforward approach of using the same rotations in different order thus would lead to different final orientations with respect to gravity, making it possible to infer the criterion of inequality of final orientations exclusively from the final graviceptive cues.

The approach used here avoids this possibility: using different sequences of rotation, subjects were rotated from the same initial orientation (upright, see Fig. 1 left panel) to various supine orientations, which were identical with respect to gravity (Fig. 1 right panels). Therefore, gravity cues in the final position could not be used to distinguish orientations. However, final subject orientations differed with respect to the angle \(\alpha\) within the earth-horizontal plane (e.g., different sequences of rotation from upright facing north to supine with the head pointing either west or east). Subjects were then instructed to indicate their remembered initial orientation in the earth-horizontal plane. We hypothesized that if the required path integration process takes into account the non-commutativity of rotations, the same final orientation should correctly be perceived as being equal despite different paths taken to get there, but different final orientations should be distinguished despite equal graviceptive cues.

Preliminary results were reported earlier in abstract form (Glasauer et al. 1996).

\(^1\) Path integration usually refers to the temporal integration of self-velocity to yield self-displacement. However, in accordance with the original definition (Mittelstaedt & Mittelstaedt 1980), we suggest that any process is termed path integration, if it yields self-displacement from idiothetic cues such as self-velocity (temporal integration) or instantaneous displacement (spatial integration).
Methods

Experiments

Ten healthy subjects (2 females, 8 males, 25-41 years) without a history of vestibular or ocular motor problems gave their informed consent to participate in the present experiment, which conformed to the standards set by the Declaration of Helsinki. Subjects sat upright in a two-axis rotating chair (SEGA), initially always facing the same space-fixed direction in the horizontal plane (Fig. 1 left, defined as \( \alpha = 0^\circ \)). During the experiment, subjects were rotated in complete darkness to six supine orientations (Fig. 1, right). The supine orientations differed by the final orientation \( \alpha \) in the horizontal plane, i.e., by the angle between the initial facing direction and the final longitudinal body axis. The final angles \( \alpha \) with respect to the initial orientation were \( \pm 80^\circ, \pm 90^\circ, \) and \( \pm 100^\circ \). The two-axis rotating chair consists of a gimbal system with the inner subject-fixed axis parallel to the subject’s naso-occipital roll axis, and the outer earth-fixed axis is earth-horizontal (Fig. 1). Subjects, secured by safety belts and a head restraint, sat within a cabin that was closed throughout the experiment to shield subjects from airflow and any residual external light. Additionally, the laboratory was darkened throughout the experiment. To mask external sounds, subjects wore headphones, which delivered white noise.

To test for path independence, three different rotations were performed to bring subjects from the initial orientation into the final orientations (Fig. 2): 1) pitch-roll: the subject was first pitched back by \( 90^\circ \) into the supine position, and then rolled around the naso-occipital axis by the angle \( \alpha \) (\( \pm 80^\circ, \pm 90^\circ, \) and \( \pm 100^\circ \)) to reach the final orientation; 2) roll-yaw: the subject was first rolled around the angle \( \alpha \) (\( \pm 80^\circ, \pm 90^\circ, \) and \( \pm 100^\circ \)) and subsequently rotated around the earth-horizontal axis by \( +90^\circ \) or \( -90^\circ \) to reach the supine position (for \( \alpha = \pm 90^\circ \), this is a pure yaw rotation); 3) combined: the rotation was performed by rotating both axes of the chair at
approximately the same time; this yielded an oblique time-varying axis of rotation due to the
different peak velocities of the two axes (inner axis peak velocity 100°/s, outer axis 60°/s) and
final orientations equal to those of pitch-roll and roll-yaw. All rotations were done with
trapezoidal velocity profiles (see Fig. 2). Rotations were performed in randomized order.

Figure 2

Figure 2 shows subject positions (as insets) for the three rotations together with the angular
velocity stimuli in egocentric coordinates, i.e., the angular velocity as sensed by the vestibular
system. Each subject underwent 6*3=18 rotations in randomized order.

Before each rotation, subjects were asked to remember their orientation in the earth-horizontal
plane (see Fig. 1 left), i.e., their heading or straight-ahead direction (e.g., looking north while
being in the initial position). After each rotation (duration <5s, see Fig. 2) the supine subjects
had to indicate their self-orientation in space by rotating an indicator, a computer-controlled
luminous line polarized by an arrowhead and displayed on a dark TV screen, around the naso-
occipital axis by remote control. The TV screen was mounted inside the chair’s cabin in front
of the subject, i.e., the screen was always in the same position with respect to the subject. The
edges of the screen were masked by a blackboard with a circular hole, and the luminance of
the screen was dimmed so that the interior of the cabin was not visible. The subjects were
instructed to rotate the line within 30s so that it pointed along the remembered initial
orientation, as if the indicator were a compass needle (i.e., the indicator should have the same
orientation in space as the subjects’ straight-ahead before the rotation, e.g., when the initial
heading was north, the correct response would have been to rotate the indicator so that it
points north). After 30s, the chair was quickly rotated back to the initial position, and the next
trial commenced after the subjects were reminded to memorize their orientation.
Chair position and indicator setting were recorded (125 Hz) for further analysis. Statistical analysis was done on the final indicator orientation pooled for positive and negative final orientations using a repeated measures ANOVA with two within-subjects factors: orientation (80°, 90°, 100°) and path (pitch-roll, roll-yaw, combined) using Statistica 6.1 (Statsoft, Tulsa, OK).

Model simulations
To show the difference in expected responses for commutative vs. non-commutative processing, we simulated both cases. As implementation of the non-commutative model, any mathematically correct transformation from angular velocity to angular orientation is possible. In the simulations shown, we used a rotation vector model. A rotation vector describes angular orientation using only three components (Haustein 1989):

\[ r = \tan(\varphi/2) \cdot n \quad \text{Eqn. 1} \]

with \( \varphi \) being the angle of rotation around an axis \( n \). The differential equation to compute the angular orientation \( r \) from angular velocity \( \omega \) is given by (Hepp 1994):

\[ \frac{d}{dt} r = (\omega \cdot r) \cdot r + (\omega \times r) / 2 \quad \text{Eqn. 2} \]

with \( \cdot \) denoting the inner or dot product and \( \times \) the vector cross product. Eqn. 2 was used for the non-commutative simulations.

Since a commutative model is mathematically incorrect for arbitrary rotations, the model chosen was designed to fulfill two criteria. 1) The commutative model should be correct for rotations around a single axis, and 2) the angular orientation resulting from the commutative model should be a rotation vector (Eqn. 1) for easy comparison. This results in:

\[ r = \tan\left(\frac{1}{2} \cdot \int \omega \cdot dt\right) \quad \text{Eqn. 3} \]

Simulations of the models (see Results) were done using Simulink and Matlab (Mathworks, Natick, MA).
Results

Model simulation

Figure 3 depicts the model simulations for the non-commutative model (filled symbols) and the commutative model (open symbols). As expected, the non-commutative model shows veridical responses, i.e., simulated perceived orientation coincides with physical orientation (dashed line). Note that, due to the path independence of rotations, final orientations for the three paradigms overlap. In contrast, the simulations of the commutative model, which simply integrates the velocity stimulus, show a clear dependence on paradigm: while simulated responses for roll-yaw and combined rotations are comparable as expected from their similar velocity profiles (cf. Fig. 2 middle and bottom), predicted responses for pitch-roll differ from these by about 80°.

Experiment

Figure 4 shows the final indicator orientation for all ten subjects, rotational paths (Circles: pitch-roll; squares: roll-yaw; diamonds: combined), and final orientations. Seven subjects adjusted the indicator close to veridical responses (diagonal lines in Fig. 4), thus clearly showing a response which reflected their final orientation. The three remaining subjects differed in that they either responded as if they had been pitched back to the supine position only (S5, S7), i.e., they adjusted the line around 180°, or showed a mixture of responses (S8). S8 reported to be confused by the experiment and considered herself unable to solve the task. Another subject (S1) adjusted the indicator twice to the 180° position. As evident from Fig. 4, most subjects’ responses clearly differed for final body orientations with positive or negative angles (final heading at approx. 90° or 270°) within the earth-horizontal plane. To test whether the small differences between final orientations on one side
also resulted in different responses, we pooled positive and negative data from each subject. A first ANOVA including the data from all subjects showed no effect of final orientation or path. However, when subjects S5, S7, and S8, and the two outliers of S1 were excluded, a main effect of final orientation was found \[ F(2,12)=7.2, \ p=0.009 \], but no effect of path (\( p>0.7 \)) and no interaction (\( p>0.3 \)). The main effect of final orientation shows that, on average, subjects were aware even of the small differences in final self-orientation on one side, and did not just always respond with the same indicator angle irrespective of end position (Fig. 5A). Errors in estimated orientation depended on the final chair orientation with smaller errors for the 100° end position [80°: 28.5° (SE 3.9°); 90°: 18.8° (SE 4.1°); 100°: 15.4° (SE 5.0°)].

The comparison of the experimental results with the model simulations (Fig. 5B) shows that errors in perceived final orientation are much larger than expected from a perfect non-commutative model, but not depended upon rotation sequence as expected from a commutative model.

**Discussion**

The majority of our subjects were able to estimate self-orientation in the horizontal plane after being rotated into a supine position along three different paths. The estimation errors show that subjects, on average, underestimated their angular position in the horizontal plane with respect to their original orientation. The comparison of model predictions for a mathematically correct model (non-commutative model, see Methods) and a commutative model (see Methods) shows that for the commutative model estimated final orientation in the horizontal plane differed by about 80° between the pitch-roll condition and the other two conditions (Fig. 5B). The present results (Fig. 5A) show that although the estimation was inaccurate, there was no difference between experimental conditions, as expected for non-
commutative processing. In none of the subjects who were able to solve the task was a
dissociation between pitch-roll and the other two conditions observed. In fact, as shown in
Appendix 1, any commutative processing of the successive rotations would imply that the
perceived final orientations are different. Thus, our subjects were able to take the non-
commutativity of self-rotations into account, as was reported previously for gaze stabilization
by the vestibulo-ocular reflex (Tweed et al. 1999). Functionally, this remarkable ability may
prove necessary to prevent falls when making rapid simultaneous or subsequent head and
body movements. For example, bending forward by 90° while turning the head to finally look
right or left does not normally cause spatial disorientation or falls.

Three out of ten subjects (2 females, 1 male) were not able to correctly indicate their self-
orientation. Two subjects responded as if they had only been tilted back by 90°, but did so
independently of condition, that is, even for roll-yaw which involved no pitch rotation. One
subject was confused, her responses varied between correct indication, mirror indication (side
error), and pitch-back response. As none of these subjects suffered from vestibular deficits,
we hypothesize that their inability is due to a deficiency in the central processing of vestibular
self-velocity information, for example, in the ability to update self-orientation by 3D path
integration.

The orientation estimates of the remaining subjects showed errors of about 20° on average.
This raises the question of whether path-independent orientation estimates are compatible
with such large estimation errors. An underestimation of angular velocity in one of the
components, for example in roll, would lead to large differences between conditions (Fig. 5C,
open symbols), i.e., to path-dependent responses even though the processing is still non-
commutative (see Appendix 2). However, in the present case, a solution that accounts for both
path-independence and estimations errors can be found as shown in Fig. 5C (filled symbols)
by assuming differences in processing roll vs. pitch and yaw information (see Appendix 2).
Thus, the experimentally determined path-independence and estimation errors are compatible
with a non-commutative model. The weighting of the derivative of roll orientation used here is similar to that proposed earlier to explain the eye position dependence of the torsional vestibulo-ocular reflex (Tweed 1997). For visuospatial updating, it has recently been shown that the processing of roll and yaw rotations differs indeed with respect to processing of gravity as an additional cue (Klier et al. 2006).

Since three-dimensional rotations on earth necessarily involve changes in orientation with respect to gravity, there is an alternative to the exclusive use of angular velocity information. Subjects could have used gravitational cues that are sensed by the otoliths, truncal graviceptors (Mittelstaedt 1996), or somatosensation to determine their orientation with respect to gravity. However, note that the gravity cues available at the end of the rotation are not sufficient to determine the orientation in the earth-horizontal plane: subjects were in the supine position in all occasions, thus their final orientation with respect to gravity was always the same. Thus, using gravity cues for this task also requires an ongoing updating process, i.e., keeping track of the change of the direction of gravity with respect to the head. Such a solution, if implemented correctly, allows accurate estimates of self-orientation and also involves non-commutative processing of both graviceptive and angular velocity cues (see Appendix 3; predictions of this ‘projection model’ are equivalent to the non-commutative model shown in Fig. 5B). Using such processing, updating of the orientation in the earth-horizontal plane using only the changing gravity cues would be possible for the roll-yaw condition, but not for pitch-roll: Since the second rotation in the pitch-roll condition was a turn around the earth-vertical axis (coinciding with the subject’s naso-occipital axis), it should have gone unnoticed. In contrast, roll-yaw consisted of two rotations around earth-horizontal axes, thus making it possible to infer the final orientation solely from keeping track of changing graviceptive cues.

The importance of gravitational cues for orienting movements towards remembered targets has been emphasized by various recent studies (e.g., Klier et al. 2005, 2006; Prieur et al.
2005; Van Pelt et al. 2005). For example, subjects could make accurate saccades to remembered target locations after roll rotations around an earth-horizontal, but not around an earth-vertical axis (Klier et al. 2005). However, such a dissociation was not observed in the present experiments. Another study (Van Pelt et al. 2005) showed that, after intervening whole body roll rotations, errors in saccades to previously seen visual targets were not related to the intervening rotation in roll, but to body orientation with respect to gravity. This finding evidently points towards the use of gravitational cues in updating visual space, suggesting that the same may be true for estimation of self-orientation.

We conclude that whatever sensory input is used, the majority of subjects seem to be able to correctly integrate self-velocity or graviceptive cues into a consistent estimate of self-orientation in the horizontal plane, i.e., an estimate that is independent of the path taken to get to that orientation. As we have shown, such a path-independent estimate is only possible if the computation of self-orientation is non-commutative.

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Appendix

1) Non-commutativity and path independence

Rotations are non-commutative, except in the one-dimensional case. This means, if two subsequent rotations are performed in reverse order, the final orientation of the rotated object will not be the same (e.g., Tweed et al. 1999).

Consequently, temporal integration of a time varying angular velocity vector alone does not yield angular position, except in the one-dimensional case. This is because temporal integration can be expressed as the cumulative summation of the integrated variable over infinitely small time steps. Since summation is commutative, so is integration.

Thus, for temporal integration to yield angular orientation, it is not angular velocity, but the derivative of angular orientation which needs to be integrated. This derivative is computed from angular velocity and orientation (e.g., Haslwanter 1995).

In the present experiments, two sequences of different rotations (pitch-roll and roll-yaw) were performed consecutively, yielding the same final orientation. During a particular rotation, e.g., roll, the orientation of the rotation axis with respect to the subject did not change, thus each rotation was one-dimensional. Hence, for each rotation alone, one could argue that a commutative operation would suffice to estimate the final orientation with respect to the starting orientation before this particular rotation. To answer the question of whether non-commutativity is known to the brain, the concatenation of the two rotations is crucial.

The final orientation \( \underline{r} \) (underline indicates a vector) of the chair following the rotations \( \underline{r}_2 \) was

\[
\underline{r} = \underline{r}_1 \otimes \underline{r}_2 = \underline{r}_2 \otimes \underline{r}_3
\]

with \( \otimes \) denoting the concatenation of two rotations, e.g., the product of two rotation matrices or two quaternions (e.g., Haslwanter 1995). Note that \( \underline{r}_2 \), the roll rotation, appears in both sequences of rotations, since the rotating chair is a gimbal system in which the inner axis rotates the subject around the same subject-fixed roll axis in both sequences.
We will show now that, if the brain mistakenly assumed that rotations are commutative, the final orientation estimates would not be equal. That is, if the estimates of orientation for the same rotations, but in different order, were equal, then the estimates for the two sequences of different rotations shown above would not be the same.

In the following, the sign “^” indicates such estimates from commutative computations. The estimate of orientation after the sequence $r_1$ followed by $r_2$ can thus be written as

$$\hat{\mathbf{L}}_{1,2} = \mathbf{L}_1 \oplus \mathbf{L}_2$$

and that of the second sequence

$$\hat{\mathbf{L}}_{2,3} = \mathbf{L}_2 \oplus \mathbf{L}_3$$

Here we used the symbol $\oplus$ to denote any possible commutative concatenation of rotations.

Since commutativity is assumed, the order of rotations does not matter, and thus

$$\hat{\mathbf{L}}_{1,2} = \hat{\mathbf{L}}_{2,1} = \mathbf{L}_2 \oplus \mathbf{L}_1$$

Thus, both estimates $\hat{\mathbf{L}}_{1,2}$ and $\hat{\mathbf{L}}_{2,3}$ can be computed from rotation $r_2$ followed by a second rotation ($r_1$ or $r_3$, respectively). This, however, shows that the estimate $\hat{\mathbf{L}}_{1,2}$ could only be equal to $\hat{\mathbf{L}}_{2,3}$, if rotations $r_1$ and $r_3$ were equal or zero, or if the brain were mistakenly unable to distinguish between both. The first was not the case in the present experiment, and the second can be safely excluded, since it would mean that the brain cannot distinguish a 90° pitch-back rotation from a 90° yaw rotation. Thus, assuming commutativity, the two sequences would yield different orientation estimates, as had to be shown.

Note that the proof makes no assumptions about how the integration of angular velocity or concatenation of successive rotations is actually performed by the brain, i.e., the experiment shows that the brain must necessarily take into account the non-commutativity of rotations to arrive at the same final estimate of orientation. This is also the case if the computations would be performed in an earth-fixed rather than a subject-centered coordinate system. To show this, one can simply translate the subject-centered rotations into earth-fixed rotations (pitch-roll
translates to pitch-yaw, and roll-yaw translates to roll-pitch) and adopt the same line of reasoning as described above.

2) Modified non-commutative models

For simulations shown in Fig. 5C, the model in Eqn. 2 (Methods) was modified. For the underestimation of angular velocity (Fig. 3C open symbols), the roll component of angular velocity was multiplied by 0.75.

For the simulations showing estimation errors similar to actual data together with path-independence (filled symbols), the model was modified as follows:

\[ \tilde{\rho} = G \cdot (\omega + (\omega \times \tilde{\rho}) \cdot \tilde{\rho} + \omega \times \tilde{\rho}) / 2 \]

with \[ \tilde{\rho} = G^{-1} \cdot \rho, \quad G = \begin{bmatrix} 0.5 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} \]

Thus, the roll component of the derivative of orientation was weighted with 0.5, and the roll orientation used to compute the derivative was weighted by 2.

3) Projection model

Here, a mathematically correct model is derived for computing self-orientation in the earth-horizontal plane from two sensory inputs: angular velocity and gravity. Assuming that gravity \( g \) is known from graviceptive sensory input or a central gravity estimator (e.g., Glasauer & Merfeld 1997, Merfeld & Zupan 2002), the z-axis of the space-fixed coordinate system \( z \) can be expressed in subject-centered coordinates by

\[ z = \frac{g}{|g|} \]

with \( |.| \) expressing the norm of \( g \). Thus, \( z \) is a unit vector parallel to gravity.

The space-fixed coordinate axis \( z \) (within the earth horizontal plane) expressed in subject-centered coordinates can then be computed from angular velocity \( \omega \) as
\[ \dot{x} = \omega \times x \]

with \( x \) denoting the vector cross product. By decomposing angular velocity \( \omega \) into two components parallel and perpendicular to the z-axis, the x-axis can be expressed as

\[ \dot{x} = \omega_p \times x + \omega_\perp \times x \]  \hspace{1cm} \text{Eqn. 4.1} \]

The parallel component is determined by projecting the measured angular velocity vector \( \omega \) onto the z-axis:

\[ \omega_p = (\omega \cdot z) \cdot z \]  \hspace{1cm} \text{Eqn. 4.2} \]

with \( \cdot \) denoting the inner or dot product. In contrast, the cross-product \( \omega_\perp \times x \), which points along the z-axis, can be expressed solely by using the gravity-derived z-axis and its temporal derivative:

\[ \omega_\perp \times x = ((\omega \times z) \cdot x) \cdot z = (x \cdot \dot{z}) \cdot z \]  \hspace{1cm} \text{Eqn. 4.3} \]

because \( \dot{z} = \omega \times z \). Inserting Eqn. 4.2 and 4.3 in 4.1 yields:

\[ \dot{x} = (\omega \cdot z) \cdot (x \times \dot{z}) + (x \cdot \dot{z}) \cdot z \]  \hspace{1cm} \text{Eqn. 4.4} \]

from which the instantaneous direction of the x-axis \( \ddot{x} \) is determined. The first part of the equation uses angular velocity input from the semicircular canals, projects it onto the space-fixed axis parallel to gravity, and uses this earth-vertical component of angular velocity to derive that part of the change of self-orientation in the earth-horizontal plane which is related to rotations within the earth-horizontal plane. The second part relies completely on graviceptive information to derive the part of self-orientation changes related to rotations around axes perpendicular to gravity. This model, which can be conceived as space-fixed computation of self-orientation, is non-commutative as well.
References

Crawford JD, Medendorp WP, Marotta JJ. Spatial transformations for eye-hand coordination. J Neurophysiol 92:10-19, 2004


Israel I, Sievering D, Koenig E. Self-rotation estimate about the vertical axis. Acta Otolaryngol 115:3-8, 1995


Mach E. Grundlinien der Lehre von den Bewegungsempfindungen. Engelmann, Leipzig. 1875


Smith MA, Crawford JD. Implications of ocular kinematics for the internal updating of visual space. J Neurophysiol 86:2112-2117. 2001


Figure legends

**Figure 1:** Initial (left panel) and final (other panels) chair and body position for all six final orientations ($\alpha$ corresponds to the orientation in the earth-horizontal plane). Circles around the subject show the gimbal frames, the axes are indicated by beams. The screen (enlarged for clarity) is shown in front of the subject. In the final orientations, the correct response of the subject would be to orient the visual indicator as shown (black line, veridical orientation) so that it is parallel to the naso-occipital axis in the initial body position.

**Figure 2:** Subject orientation in space (insets) and angular velocity sensed by the vestibular system (i.e., angular velocity in head coordinates) during the three different rotational paradigms for final 90° orientation. Initial and final orientation of the subject was the same for all three experimental conditions shown, but the path taken was different (as shown in the insets), and so were the angular velocities sensed by the vestibular system (solid: roll, dashed: pitch, dash-dotted: yaw; all given in head coordinates). Arrows indicate the time when subjects reached the final orientation.

**Figure 3:** Predicted final orientation for mathematically correct updating of self-orientation (closed symbols, non-commutative model, all values overlap and fall on the unity line, which indicates veridical responses) and for a commutative model (open symbols). Symbols indicate the experimental condition (circles: pitch-roll, squares: roll-yaw; diamonds: combined). Predictions for the commutative model differ by more than 80° between the pitch-roll condition and the other two conditions.

**Figure 4:** Final indicator orientations plotted as a function of final subject orientation (heading) for each subject (S1-S10). Long dashed line: veridical response (equivalent to
prediction from the non-commutative model). Circles: pitch-roll; squares: roll-yaw; diamonds: combined. While most subjects showed nearly veridical responses, S5 and S7 oriented the indicator as if they had only been pitched backward (approx. 180°), and S8, who reported to be confused by the experiment, showed a mixture of normal responses, side errors (e.g., S8: pointing approx. at –90° when 90° would have been correct), and 180° responses.

**Figure 5:** A: Final indicator orientation over final heading for the three paradigms (circles: pitch-roll, squares: roll-yaw; diamonds: combined). Data for positive and negative directions are pooled together (subjects S5, S7, S8, and two outliers for S1 excluded). Dashed line (unity slope) indicates veridical response, error bars show one standard deviation. **B:** Comparison of data from A (light gray) with model simulations (see Fig. 3) of the non-commutative models (closed symbols, non-commutative model or projection model) and the commutative model (open symbols, circles: pitch-roll, squares: roll-yaw; diamonds: combined). Data are path-independent, as expected for non-commutative processing, but show considerably larger errors than perfect updating. **C:** Predicted final orientations for the non-commutative model with underestimation of angular roll velocity (open symbols) showing path-dependent errors, the modified non-commutative model which shows path-independent estimation errors (closed symbols; again values for the three conditions overlap), and data from A (light gray) for comparison. The non-commutative model with underestimation of angular roll velocity (open symbols) is no longer path-independent, and thus cannot explain the data.
Figure 1: Initial (left panel) and final (other panels) chair and body position for all six final orientations ($\alpha$ corresponds to the orientation in the earth-horizontal plane). Circles around the subject show the gimbal frames, the axes are indicated by beams. The screen (enlarged for clarity) is shown in front of the subject. In the final orientations, the correct response of the subject would be to orient the visual indicator as shown (black line, veridical orientation) so that it is parallel to the naso-occipital axis in the initial body position.
Figure 2: Subject orientation in space (insets) and angular velocity sensed by the vestibular system (i.e., angular velocity in head coordinates) during the three different rotational paradigms for final 90° orientation. Initial and final orientation of the subject was the same for all three experimental conditions shown, but the path taken was different (as shown in the insets), and so were the angular velocities sensed by the vestibular system (solid: roll, dashed: pitch, dash-dotted: yaw; all given in head coordinates). Arrows indicate the time when subjects reached the final orientation.
Figure 3: Predicted final orientation for mathematically correct updating of self-orientation (closed symbols, non-commutative model, all values overlap and fall on the unity line, which indicates veridical responses) and for a commutative model (open symbols). Symbols indicate the experimental condition (circles: pitch-roll, squares: roll-yaw; diamonds: combined). Predictions for the commutative model differ by more than 80° between the pitch-roll condition and the other two conditions.
Figure 4: Final indicator orientations plotted as a function of final subject orientation (heading) for each subject (S1–S10). Long dashed line: veridical response (equivalent to prediction from the non-commutative model). Circles: pitch-roll; squares: roll-yaw; diamonds: combined. While most subjects showed nearly veridical responses, S5 and S7 oriented the indicator as if they had only been pitched backward (approx. 180°), and S8, who reported to be confused by the experiment, showed a mixture of normal responses, side errors (e.g., S8: pointing approx. at -90° when 90° would have been correct), and 180° responses.
Figure 5: A: Final indicator orientation over final heading for the three paradigms (circles: pitch-roll, squares: roll-yaw; diamonds: combined). Data for positive and negative directions are pooled together (subjects S5, S7, S8, and two outliers for S1 excluded). Dashed line (unity slope) indicates veridical response, error bars show one standard deviation. B: Comparison of data from A (light gray) with model simulations (see Fig. 3) of the non-commutative models (closed symbols, non-commutative model or projection model) and the commutative model (open symbols, circles: pitch-roll, squares: roll-yaw; diamonds: combined). Data are path-independent, as expected for non-commutative processing, but show considerably larger errors than perfect updating. C: Predicted final orientations for the non-commutative model with underestimation of angular roll velocity (open symbols) showing path-dependent errors, the modified non-commutative model which shows path-independent estimation errors (closed symbols; again values for the
three conditions overlap), and data from A (light gray) for comparison. The non-commutative model with underestimation of angular roll velocity (open symbols) is no longer path-independent, and thus cannot explain the data.