Velocity Storage Contribution to Vestibular Self-Motion Perception in Healthy Human Subjects

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Bertolini G, Ramat S, Laurens J, Bockisch CJ, Marti S, Straumann D, Palla A. Velocity storage contribution to vestibular self-motion perception in healthy human subjects. J Neurophysiol 105: 209–223, 2011. First published November 10, 2010; doi:10.1152/jn.00154.2010. Self-motion perception after a sudden stop from a sustained rotation in darkness lasts approximately as long as reflexive eye movements. We hypothesized that, after an angular velocity step, self-motion perception and reflexive eye movements are driven by the same vestibular pathways. In 16 healthy subjects (25–71 years of age), perceived rotational velocity (PRV) and the vestibulo-ocular reflex (rVOR) after sudden decelerations (90°/s²) from constant-velocity (90°/s) earth-vertical axis rotations were simultaneously measured (PRV reported by hand-lever turning; rVOR recorded by search coils). Subjects were upright (yaw) or 90° left-ear-down (pitch). After both yaw and pitch decelerations, PRV rose rapidly and showed a plateau before decaying. In contrast, slow-phase eye velocity (SPV) decayed immediately after the initial increase. SPV and PRV were fitted with the sum of two exponentials: one time constant accounting for the semicircular canal (SCC) dynamics and one time constant accounting for a central process, known as velocity storage mechanism (VSM). Parameters were constrained by requiring equal SCC time constant and VSM time constant for SPV and PRV. The gains weighting the two exponential functions were free to change. SPV were accurately fitted (variance-accounted-for: 0.85 ± 0.10) and PRV (variance-accounted-for: 0.86 ± 0.07), showing that SPV and PRV curve differences can be explained by a greater relative weight of VSM in PRV compared with SPV (twofold for yaw, threefold for pitch). These results support our hypothesis that self-motion perception after angular velocity steps is driven by the same central vestibular processes as reflexive eye movements and that no additional mechanisms are required to explain the perceptual dynamics.

INTRODUCTION

Maintaining visual acuity while moving the head depends mainly on the contribution of the vestibulo-ocular reflex (VOR), which stabilizes gaze in space. For instance, during brief head rotations, the rotational VOR (rVOR) ensures clear vision by evoking compensatory eye movements of roughly equal velocity as the head, but in the opposite direction. During sustained head rotations in darkness, the rVOR response decays with a time constant that is considerably longer (10–30 s) than what is predicted from the activity of the vestibular afferents (3–7 s) from the semicircular canals (SCCss) (Blanks et al. 1975; Büttner and Waespe 1981; Cohen et al. 1981; Dai et al. 1999; Fernandez and Goldberg 1971; Gizzarelli and Harper 2003; Leigh and Zee 2006). It is believed that the prolongation of the afferent signal is achieved by a neural mechanism, called the velocity storage mechanism (VSM), which presumably involves the nucleus prepositus hypoglossi and the medial vestibular nuclei (Leigh and Zee 2006; Raphan et al. 1977; Robinson 1977a). The functional significance of the VSM is not yet fully understood, but several properties of the VSM have been identified. Among others, the VSM improves the ability of the rVOR to compensate head velocity at low frequencies (Raphan et al. 1979; Robinson 1977a). The VSM may also contribute to the mechanisms of spatial orientation, as suggested by postrotatory tilting experiments in primates and nonprimates: when the head is tilted with respect to gravity after the sudden stop from a sustained rotation in darkness, the eye velocity vector tends to realign toward the gravito-inertial acceleration vector (i.e., the resultant of gravity and linear acceleration) (Angelaki and Hess 1994; Dai et al. 1991; Harris 1987; Merfeld et al. 1993b; Raphan and Cohen 1988, 2002; Raphan et al. 1981; Wearne et al. 1997, 1998; Yasuda et al. 2002, 2003). This reorientation of the ocular rotation axis on head tilting is, however, relatively weak or missing in humans (Bockisch et al. 2005; Fetter et al. 1992, 1996; Harris and Barnes 1987). The VSM is also believed to enhance and perpetuate optokinetic nystagmus elicited by sustained movement of the visual field. Thus optokinetic after-nystagmus, i.e., continuing nystagmus in total darkness after optokinetic stimulation, is generated by the VSM (Cohen et al. 1977; Raphan et al. 1977; Robinson 1977b). Finally, it has been hypothesized that the VSM may be involved in the segregation of tilt and translation (Angelaki et al. 1999; Glasauer 1995; Green and Angelaki 2003, 2004; Mayne 1974; Merfeld et al. 1999, 2001; Young 1974; Zupan et al. 2000), because the ototholiths, as with any linear accelerometer, cannot distinguish between inertial and gravitational acceleration (Einstein 1907).

Vestibular signals provide not only the input for ocular and spinal motor reflexes, but also contribute to higher-level cortical processes such as motion perception. For instance, in total darkness, sudden velocity changes, i.e., velocity steps, after a period of constant-velocity rotation elicit vestibular nystagmus and a perception of self-motion. Like the slow-phase eye velocity of per- or postrotatory nystagmus, perceived rotational velocity decays slower than the activity of the SCC afferents (Guedry 1974; Young 1983). By comparing the overall duration of rotational sensation and nystagmus evoked by rotational velocity steps, earlier studies found disparities between subjective and objective responses. Vestibular nystagmus was reported to have a longer duration and a higher threshold than self-motion perception (Benson 1968; Jongkees 1974; Melvill Jones et
al. 1964; Stahle 1957; Van Egmond et al. 1948). Besides the lack of simultaneous recordings of perception and nystagmus and the acknowledged analytical difficulties in determining the thresholds, the disparities were assumed to be the results of different adaptive processes for perception and reflexive eye movements (Benson 1968; Groen 1957; Stahle 1957). These differential adaptive processes, however, were not further explored. More recent studies, in contrast, have consistently observed similar durations and decay characteristics for slow-phase eye and perceived rotational velocities (Okada et al. 1999; Sinha et al. 2008). As a result, Okada et al. (1999) speculated that a central process comparable to the VSM of the rVOR also exists at a perceptual, presumably cortical, level. Recently, in patients with dysfunction of the vermal cerebellum, a neural structure known to influence the VSM of the rVOR, Bronstein et al. (2008) found comparable modifications of nystagmic and perceptual responses, pointing at a possible role of these structures also in the percept of self-motion. The details of this central processing on the percept of self-motion, however, have not been further studied.

The relation between reflexive responses and conscious perception also increasingly sparks interest because of reports on linear motion suggesting that qualitatively different mechanisms are involved in generating ocular reflexes and sensory responses (Merfeld et al. 2005a,b; Park et al. 2006). Specifically, whereas reflexive eye movements show an accurate compensation during high-frequency translations, which decreases with declining stimulus frequency, perception of translation typically is more robust even at low frequencies. This leads to the speculation that reflexive and perceptual mechanisms are processed in different ways. On the other hand, other reports cast doubts on the aforementioned hypothesis, because in the near absence of nondirectional cues, such as noise and vibration, perception of translation has shown to exhibit dynamic properties similar to those of reflexive eye movements (Au Yong et al. 2007; Seidman 2008; Seidman et al. 2009). Rather, differences in perception and reflexive eye movements have been attributed to cognitive influences, meaning that subjects are subconsciously influenced by nonvestibular cues. Of course it is important to emphasize that the exposure to rotational and linear movements pose different demands on reflexive and perceptual responses and thus are not directly comparable. Nevertheless, these discrepancies necessitate further studies on how the brain processes vestibular ocular motor and perceptual information.

In this study, we aimed to characterize the dynamics of rotational self-motion perception in healthy subjects during velocity steps of a turntable rotating about the earth-vertical yaw axis (i.e., subjects sitting in upright position) and about the earth-vertical pitch axis (i.e., subjects lying in 90° left ear down position). The response of the rVOR to a velocity step can be accurately simulated by the sum of two exponential functions, with a time constant accounting for peripheral (i.e., SCC) and with a time constant accounting for central (i.e., VSM) dynamics. Because the SCC input elicited by a velocity step is identical for the rVOR and for self-motion perception and because the durations of nystagmus and of self-motion perception seem to be similar, we asked whether perceived rotational velocity could be accurately fitted by the same exponential functions with equal time constants, thereby hypothesizing that the rVOR and self-motion perception could share the same central mechanisms that perpetuate peripheral SCC signals.

Two equivalent models explain the dynamics of the rVOR in response to a velocity step with two exponentials: the Raphan, Cohen, and Matsuo model (Raphan et al. 1977) and the Robinson model (Robinson 1977a). These models are considered mathematically indistinguishable, because they provide the same input–output relationship. The physiological hypotheses behind the two models, however, are different as reflected by their structures and parameters (Demer and Robinson 1983). The Raphan, Cohen, and Matsuo model assumes that the rVOR velocity command results from the sum of two separate pathways: one direct pathway that carries SCC afferent signals directly to the ocular motor neurons and one indirect pathway that processes the SCC afferent signal through an integrator with a negative feedback loop, which represents the VSM. In contrast, the Robinson model consists of a single pathway with the VSM activity modeled as a positive feedback loop along this pathway. For a graphical representation of both models, see Fig. 1, A and B (structures and pathways drawn with solid lines).

Note that the fitting procedure for the step responses of slow-phase eye velocity and perceived rotational velocity is independent from the underlying model, i.e., this study does not to favor one of the two models. Our prediction on how the perception output can parallel the rVOR output in the two models, assuming that the two time constants for slow-phase eye velocity and perceived rotational velocity are equal, is depicted in Fig. 1, A and B (dashed line). The signal flow for perception implies that even if the two time constants for slow-phase eye velocity and perceived rotational velocity are equal, the strength of the different pathways are free to change. A detailed description of both models and our predictions about the perceptual output is provided in Appendix A.

Our choice of studying self-motion perception with these two models depends on the aim of our study: understanding whether perceived rotational velocity can be accurately described by the same simple input (i.e., vestibular organs) – output (i.e., oculomotor response) relationship that explains rVOR responses without postulating prior knowledge about the internal state of the system. We specifically decided not to consider other models based on more general concepts of system analysis, such as internal models (Borah et al. 1988; Bos and Bles 2002; Droulez and Cornilleau-Peres 1993; Droulez and Darlot 1989; Glasauer and Merfeld 1997; Laurens and Droulez 2007; Merfeld 1993a, 1995; Oman 1982; Zupan et al. 1994). For an overview about the conceptual ideas and the advantages and drawbacks of each modeling technique, see MacNeilage et al. (2008).

METHODS

Subjects

Sixteen healthy human subjects (8 female; 25–71 yr old) participated in this study. Informed consent of all subjects was obtained after full explanation of the experimental procedure. The protocol was approved by a local ethics committee and was in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki for research involving human subjects.
**Experimental setup**

Subjects were seated upright on a turntable with three servo-controlled motor-driven axes (prototype built by Acutronic). The head was restrained with an individually molded thermoplastic mask (Sinmed, Reeuwijk, The Netherlands). Subjects were positioned so that the intersection of the interaural and naso-occipital axes was at the intersection of the three axes of the turntable. Pillows and safety belts minimized movements of the body.

**Experimental protocol**

Fourteen subjects were rotated in complete darkness about the earth-vertical axis while seated upright (yaw rotation with predominant horizontal SCC activation) or lying on their left side (pitch rotation with predominant vertical SCC activation). Two subjects were rotated about the earth-vertical yaw axis only because of motion sickness or discomfort during earth-vertical pitch rotations. Within the same session, recordings were restricted to a maximum of four trials of yaw and four trials of pitch rotations, as habituation of the rVOR and of the sensation of self-rotation takes place as soon as after 10 consecutive trials of steps of angular velocity about the yaw axis (Clément et al. 2008). By restricting the number of trials, we also avoided effects of decreasing alertness. Because of the limited number of rotation trials and to investigate the reproducibility of the perceptual response, passive rotations were delivered only in counterclockwise direction (i.e., positive rotation about the upward pointing space-fixed z-axis according to the right-hand rule; Haustein 1989) at a constant angular velocity of 90°/s for the duration of 90 s. In the left side down position, this results in a backward rotation. The turntable was accelerated and decelerated at 90°/s². Postrotatory recording in darkness continued until nystagmus (rightward beating in upright position and downward beating in 90° left ear down position) decayed to zero and subjects indicated that their perception of rotational motion had vanished. Yaw and pitch rotation trials were pseudorandomly intermingled for each subject. Between rotation trials, a 30 s break was given where the test room was illuminated.
Recording of eye movements

Three-dimensional eye movements were recorded monocularly with scleral search coils (Skalar Instruments, Delft, The Netherlands) after anesthetizing the conjunctiva with 0.4% oxybuprocaine. Search coil anuli were calibrated with a method described elsewhere (Straumann et al. 1995). A turntable-fixed aluminum coil frame (side length, 0.5 m) surrounded the head and generated three orthogonal digitally synchronized magnetic wave fields of 80, 96, and 120 kHz. A digital signal processor computed a fast Fourier transform in real time on the digitized search coil signal to determine the voltage induced on the coil by each magnetic field (system by Primelec, Regensdorf, Switzerland). Coil orientation could be determined with an error of <7° over a range of ±30° and with a noise level of <0.05° (root mean squared deviation). Eye and turntable position signals were digitized at 1,000 Hz per channel with 16-bit resolution and stored on a computer hard disk for off-line processing.

Recording of rotational self-motion perception

Subjects were asked to turn a lever attached to a potentiometer that was fixed to the chair. The instruction was to match the rate of lever spinning with the perceived rotational velocity and to stop spinning when the rotation was not felt anymore (i.e., when the sensation of rotation was strong subjects should spin the lever quickly, when the sensation of rotation diminished subjects should indicate this by turning the lever more slowly, and when the subjects no longer felt the rotation they should stop spinning the lever). All subjects were right handed and turned the lever with their right hand.

This method of assessing rotational self-motion perception belongs to the method of direct measures of subjective angular velocity (Guedry 1974). It permits the comparison of relative magnitudes during the time course of a single response and, thus allows investigating whether perceived angular velocity is sensed as constant, increasing, or decreasing. Notably, however, it does not allow estimating the real magnitude of perceived angular velocity.

To avoid additional sensory cues (e.g., vibration from the chair, airflow, auditory cues), white noise was delivered through headphones and only postrotatory responses were analyzed (Okada et al. 1999). Experimental instructions were always given by the same experimenter (A.P.) to guarantee consistent information among all subjects. Signals were digitized at a frequency of 1,000 Hz with 16-bit resolution and stored on a computer hard disk for off-line processing.

To familiarize the subjects with the lever spinning task and to obtain information about the subjects’ ability to perform the motor task of lever spinning, a pretest control trial with an acoustic stimulus was performed (for a detailed description about the sound recording and a typical subject example see APPENDIX B). Before the experimental recording, additionally, one trial of leftward yaw velocity step (same stimulus parameters as used during the experimental recording) was delivered, and subjects were asked to sense the rotation but not to turn the lever yet.

Data analysis

PREPROCESSING. Data were processed on a PC using interactive programs written in MATLAB (The Mathworks, Natick, MA), version 7.5. From the search coil raw signals and calibration values, we computed the angular position of the eye in degrees. Eye velocity traces, i.e., the derivative of eye position, were further processed to reconstruct the profiles of slow phase eye velocity. To this end, the fast phases of the response were interactively marked using a custom-made MATLAB routine. After removal of the fast phases, the remaining velocity signal was linearly interpolated.

The potentiometer transduced angular position of the lever over −5 to +5 V. Calibration was obtained at each trial by taking the maximum and the minimum voltages and converting them to 0–360°. Noise was removed by low-pass filtering the eye position and potentiometer signal with a Butterworth filter with cut-off frequency of 40 Hz. Perceived rotational velocity was obtained by computing the derivative of the potentiometer signal after removing the discontinuities occurring at each turn between 360 and 0°.

The onset point of each postrotatory trial was set at the turntable stop, which was automatically detected from turntable velocity recording. The late response of perceived rotational velocity traces did not smoothly decay toward zero in all our subjects. Specifically, when subjects abruptly stopped turning the lever at a velocity >20% of the maximal velocity (referred to as a drop, see RESULTS), the fitting procedure included an offset value that was set by visual inspection to the perceived rotational velocity value immediately before this drop.

For balancing the contribution of slow-phase eye velocity and perceived rotational velocity responses in the error function of the optimization algorithm, all traces were normalized to their own peak values. Peak values were determined by filtering the traces with a 2-s median window. Scaling factors therefore differed between slow-phase eye velocity and perceived rotational velocity within each subject and among subjects. The scaling ratio between perceived rotational velocity and slow-phase eye velocity ranged within 5:15 over all subjects. Intrasubject maximum trial-to-trial variability of scaling factors was, however, consistent (range from 1:1.25). Mean slow-phase eye velocity (±SD) over all subjects was 54.9 ± 9.6°/s for yaw and 38.6 ± 11.6°/s for pitch rotations, whereas mean perceived rotational velocity was 690.5 ± 311.4 and 755.4 ± 403.2°/s, respectively. Note that the velocity of perceived rotation represents an arbitrary value, because it is a subjective estimate of the intensity or magnitude of rotation.

PARAMETER ESTIMATION. Slow-phase eye velocity and perceived rotational velocity traces from each trial were fitted to the following equations

\[
\dot{\theta}_\text{eye} = k_{0,\text{eye}} e^{-\theta_c/\tau_c} + k_{1,\text{eye}} \frac{\tau_c \tau_{\text{VSM}}}{\tau_c - \tau_{\text{VSM}}} (e^{-\theta_c/\tau_c} - e^{-\theta_c/\tau_{\text{VSM}}})
\]

\[
\dot{\theta}_\text{perception} = k_{0,\text{perception}} e^{-\theta_c/\tau_c} + k_{1,\text{perception}} \frac{\tau_c \tau_{\text{VSM}}}{\tau_c - \tau_{\text{VSM}}} (e^{-\theta_c/\tau_c} - e^{-\theta_c/\tau_{\text{VSM}}})
\]

where \(\tau_c\) and \(\tau_{\text{VSM}}\) are the time constants of the SCC transduction and of the central processing (i.e., VSM) along the vestibular pathway, and \(k_{0,\text{eye}}\) and \(k_{0,\text{perception}}\) are the gains of slow-phase eye velocity and perceived rotational velocity, respectively.

The following constraints on the set of parameters were made. 1) Within all trials of one testing session (i.e., yaw and pitch together), the same \(\tau_c\) was used to fit slow-phase eye velocity and perceived rotational velocity, based on the assumption that the peripheral time constant, representing SCC activity, is equal for both eye and perception data and does not vary within the same subject from trial to trial. 2) Within each trial of yaw and pitch turntable rotations, the same \(\tau_{\text{VSM}}\) was used to fit slow-phase eye velocity and perceived rotational velocity. 3) Within each trial of yaw and pitch turntable rotation, gain elements \((k_{0,\text{eye}}, k_{0,\text{perception}})\) were free to change to account for the differences in the dynamic characteristics of eye and perception data. Parameters

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Equation 1 represents the step responses of the two main models of the rVOR proposed by Raphan, Cohen, and Matsuo (Raphan et al. 1977a) and by Robinson (Robinson 1977), modified to include our assumption on additional perceptual output pathways. A graphic representation of the two models is given in Fig. 1, A and B (dashed lines show presumed perceptual pathways). In contrast to the original description of the Robinson model, the gain on the feedback path has been moved after the leaky integrator and two compensating signs have been changed (the minus along the direct pathway and the minus in the feedback line). This simplifies the understanding of the model without affecting the results. For a mathematical description of the original and modified models, see Appendix A.

STATISTICAL ANALYSIS. In each subject, the means of time constants and of gain ratios over all yaw and over all pitch trials were calculated. The Lilliefors test was first used to test whether the means followed a normal distribution. Repeated-measure one-way ANOVA and post hoc Holm-Sidak adjustment to compensate for multiple comparisons were performed on mean time constants and mean gain ratios between and within subject groups and conditions. A measure of the goodness of fit was provided by the variance-accounted-for technique (Galiana et al. 1995). In addition, Bayesian information criterion was computed as a measure of the adequacy of model complexity (Schwarz 1978). Whereas the variance-accounted-for measure provides a goodness of fit criterion that is independent of the number of parameters in the fitting model, the Bayesian information criterion takes the number of parameters into account, penalizing more complex models. Variance-accounted-for values should be larger to indicate a superior model, the Bayesian information criterion takes the number of model parameters, MSE is the mean squared error, and $\sigma_{\text{err}}^2$ is the variance of the error.

RESULTS

Qualitative characteristics

Figure 2 shows the main characteristics of horizontal slow-phase eye velocity (top row) and perceived rotational velocity (bottom row) after a sudden stop from a counterclockwise constant velocity rotation about the earth-vertical yaw axis in a typical subject (H.M.). Horizontal slow-phase eye velocity shows an almost immediate rise followed by a plateau-like phase (Fig. 2A). Perceived rotational velocity also rises rapidly but is followed by a plateau-like phase (Fig. 2C). The duration of slow-phase eye velocity is slightly longer than the duration of perceived rotational velocity. These typical characteristics are also seen in perceived rotational velocity and vertical slow-phase eye velocity responses after a sudden stop from a counterclockwise constant velocity rotation about the earth-vertical pitch axis (data not shown). Because slow-phase eye velocity and perceived rotational velocity traces were highly consistent on repetition in both yaw (Fig. 2, A and C) and pitch planes, the means of slow-phase eye velocity and perceived rotational velocity traces over all yaw and over all pitch repetitions for each subject are plotted in Figs. 3 and 4.

\[
BIC = \frac{N}{\sigma_{\text{err}}^2} \left( MSE + \log(N) \right) - \frac{d}{N}
\]

where $N$ is the overall number of data points, $d$ is the number of model parameters, $MSE$ is the mean squared error, and $\sigma_{\text{err}}^2$ is the variance of the error.
Eye velocity traces (Fig. 3, left) were consistent between subjects and the main characteristics of perceived rotational velocity (Fig. 3, right). However, a closer analysis of the early response of perceived rotational velocity traces showed distinct differences. In 10 subjects, perceived rotational velocity decayed by <10% of the maximum sensation within the first 5 s after both yaw (Fig. 3B) and pitch (Fig. 3F) rotations, because of a plateau-like onset-phase. In the remaining subjects, however, perceived rotational velocity decreased considerably faster (i.e., >10% of its maximum value within 5 s after turntable stopping. C, D, G, and H: short plateau group, i.e., PRV decrease of >10% of its maximum value within 5 s after turntable stopping. A, B, E, and F: long plateau group, i.e., perceived rotational velocity decrease of <10% of its maximum value within 5 s after turntable stopping.

To study whether the perceptual plateau and drop were related to the apparatus used to report perceived angular velocity or because of skeleto-motor factors, we examined the data recorded from sound trials, in which subjects were asked to match the decrease of an exponentially decaying sound (see Appendix B) by turning the lever. None of the subjects showed a plateau but in six subjects a drop was found. These were the same six subjects who showed a perceptual rotational velocity drop (5 subjects with a drop in both yaw and pitch; 1 subject with a drop in pitch only). Anticipating our conclusions, we therefore infer that the perceptual plateau is not caused by technical or skeleto-motor factors.
motor factors, whereas the drop possibly might be. Specifically, we hypothesize that the drop reflects less ability to transform the sensation of rotation into motor performance in some subjects (see Discussion).

Summarizing the qualitative impression thus far, slow-phase eye velocity and perceived rotational velocity seem to have different dynamics, although the duration of their decay is similar. In the following, we study whether—despite the dynamic differences—slow-phase eye velocity and perceived rotational velocity can accurately be fitted using two different weighted sums of the same two exponential functions (see Eq. 1 in Methods).

Quantitative analysis

Figure 5 shows slow-phase eye velocity and perceived rotational velocity responses (gray traces) after one trial of earth-vertical yaw rotation in the same subject as in Fig. 2 together with the corresponding fitted curves. The function (Eq. 1) that generates the curves that best fit slow-phase eye velocity and perceived rotational velocity (bold traces) can be divided into two components: 1) a single exponential with a time constant $\tau_C$ accounting for the SCC activity (thin trace) and 2) the difference of two exponentials with two different time constants, $\tau_C$ and $\tau_{VSM}$, representing the central processing termed VSM (dashed traces).
To test the hypothesis of whether the rVOR and self-motion perception could be modeled with the same internal time constant (i.e., the VSM), in parameter estimation, we constrained slow-phase eye velocity and perceived rotational velocity to be fitted with equal $\tau_V$ and equal $\tau_{\text{VSM}}$. The goodness of fit (variance-accounted-for) over all subjects was $0.86 \pm 0.10$ for slow-phase eye velocity and $0.84 \pm 0.06$ for perceived rotational velocity during yaw rotations and $0.86 \pm 0.11$ for slow-phase eye velocity and $0.87 \pm 0.06$ for perceived rotational velocity during pitch rotations. To evaluate the appropriateness of the model complexity, Bayesian information criterion values were additionally calculated by pooling rVOR and perception traces. With six model parameters mean Bayesian information criterion over all subjects was $78.5$ for yaw and $53.1$ for pitch rotations, indicating a significant ($P < 0.005$) correlation. For comparison, $\tau_{\text{VSM}}$ values resulting from the model constrained to six parameters, i.e., when using the same $\tau_{\text{VSM}}$ in rVOR and self-motion perception, is also plotted in Fig. 6 (white bars).

In the following, we provide a detailed quantitative analysis of the parameters obtained by the model fit in all subjects. Note that, because of the constraint of using equal $\tau_V$ and equal $\tau_{\text{VSM}}$ for slow-phase eye velocity and perceived rotational velocity, differences between reflexive eye movement and self-motion perception traces result only from differences in the ratios $R$ of the gains of the VSM component ($k_i$) to the gains of the SCC component ($k_0$). $R_{\text{VOR}}$ is the ratio of the gains ($k_{\text{eye}}/k_{\text{eye}}$) that generates the characteristic shape of the slow-phase eye velocity curve and $R_{\text{Perception}}$ is the ratio that is responsible for the characteristic shape of the perceived rotational velocity curve ($k_{\text{perception}}/k_{\text{perception}}$).

**YAW VELOCITY STEPS.** Mean $\tau_V^\text{yaw}$ ($\pm SD$) over all subjects was $5.6 \pm 1.2$ s, whereas mean $\tau_{\text{VSM}}^\text{yaw}$ ($\pm SD$) was $15.5 \pm 5.0$ s.
$R_{VOR}$ was significantly lower than $R_{perception}$ ($R_{VOR} \pm SD: 0.14 \pm 0.06$; $R_{perception} \pm SD: 0.26 \pm 0.13$; $P < 0.001$).

Because we found qualitative differences among subjects in the early and late decay responses of perceptual traces, we classified traces based on the existence of a plateau and a drop. Combining these two criteria, subjects clustered in three groups: a short plateau and no drop group ($n = 6$), a long plateau and no drop group ($n = 5$), and a long plateau and drop group ($n = 5$; Figs. 3 and 4). Repeated-measure one-way ANOVA showed a significant main effect of $\tau_{VSM}$ [$F(3) = 5.66; P < 0.02$] and $R_{perception}$ [$F(3) = 4.03; P < 0.04$] but not of $\tau_{C}$ and $R_{VOR}$. $\tau_{VSM}$ and $R_{perception}$ were significantly lower in the short plateau and no drop group compared with the long plateau and no drop and the long plateau and drop groups ($P < 0.04$ and $P < 0.03$, respectively). The long plateau and no drop and long plateau and drop groups did not significantly differ in any parameter. Estimated parameters are presented as mean in Table 1.

### PITCH VELOCITY STEPS

Mean $\tau_{C}$ over all 14 subjects was $5.5 \pm 1.2$ and mean $\tau_{VSM}$ was $6.3 \pm 3.3$. $R_{VOR}$ was significantly lower than $R_{perception}$ ($R_{VOR} \pm SD: 0.09 \pm 0.06$; $R_{perception} \pm SD: 0.31 \pm 0.19$; $P < 0.001$).

As for yaw rotations, subjects were divided into three groups. Except for one subject (F.G.), who was assigned to the long plateau and drop group for pitch rotations, all other subjects were distributed among the same groups as for yaw rotations, i.e., showed the same early and late response characteristics of perceived rotational velocity for both yaw and pitch rotations. Repeated-measure ANOVA showed a significant main effect in $R_{perception}$ [$F(3) = 7.03; P < 0.01$] only. Specifically, $R_{perception}$ was significantly lower in the short plateau and no drop group compared with the other two groups ($P < 0.05$). Estimated parameters are presented as mean $\pm SD$ in Table 1.

### COMPARISON OF YAW AND PITCH VELOCITY STEPS

Over all subjects, mean $\tau_{VSM}$ was significantly longer for yaw rotations than for pitch rotations (yaw: $15.5 \pm 5.0$; pitch: $6.3 \pm 3.3$; $P < 0.001$). Recall that parameter estimation was obtained by constraining the fit to use equal $\tau_{C}$ for yaw and pitch rotations [the slightly different mean $\tau_{C}$ overall subjects for yaw ($5.6 \pm 1.2$) compared with pitch ($5.5 \pm 1.2$) rotations is because of the fact that we tested two more subjects during yaw rotations]. $R_{VOR}$ was significantly larger (mean $\pm SD$: $R_{VOR}$ yaw: $0.14 \pm 0.06$; pitch: $0.09 \pm 0.06$; $P < 0.04$) in yaw than in pitch rotations, whereas $R_{perception}$ was not significantly different ($R_{perception}$: yaw: $0.26 \pm 0.13$; pitch: $0.31 \pm 0.19$).

In conclusion, differences between slow-phase eye velocity and perceived rotational velocity responses to steps of angular velocity over all subjects and independent of the rotation plane (i.e., yaw or pitch) can be explained by an increased relative weighting of the central VSM activity in perceived rotational velocity (i.e., $R_{perception}$ is larger than $R_{VOR}$). Moreover, the variation of $R_{perception}$ describes the differences observed in the early perceived rotational velocity response (i.e., the short vs. long perceptual plateau). In contrast, changes of the late decay response (i.e., drop vs. no-drop) do not further affect estimated parameters. Finally, the shorter $\tau_{VSM}$ is, as expected, the main difference between yaw and pitch trials.

### DISCUSSION

We studied the rVOR and rotational self-motion perception after a sudden stop from a sustained rotation about the earth-vertical axis (response to a step of angular velocity), whereas healthy subjects were either seated in upright position (earth-vertical yaw rotation) or were lying on their left side (earth-vertical pitch rotation). Slow-phase eye velocity and perceived rotational velocity responses were similar in duration both after earth-vertical yaw rotations and after earth-vertical pitch rotations. The curves of slow-phase eye velocity and perceived rotational velocity in the same trials, however, were different. Whereas slow-phase eye velocity decreased immediately after a rapid increase, perceived rotational velocity showed a plateau phase after the initial rise. In some subjects, moreover, there was a sudden drop of the late perceptual response from a consistent perceived rotational velocity level to zero.

Diversities in the curves of slow-phase eye velocity and perceived rotational velocity have been previously reported for angular velocity steps after earth-vertical yaw rotations (Sinha et al. 2008). Using different experimental techniques to signal self-motion perception (pushing button, dial with and without discrete steps), Sinha et al. (2008) consistently observed a perceptual plateau and thus concluded that it was not caused by a bias introduced by the experimental technique itself. Likewise, to study whether the perceptual plateau resulted from the signaling (instrument or factors of motor control) of self-motion perception, we asked our subjects to match the decrease of a sound by turning the same lever used to report self-motion perception during angular velocity steps. All our subjects were able to reproduce the sharp peak followed by an immediate decrease of the sound (see Appendix B for examples). We therefore infer that the perceptual plateau is not a direct consequence of the skeletal-motor action needed to spin the lever or experimental setup but rather represents a characteristic of self-motion perception.

An interesting behavior was observed during the late part of the perceptual response. In contrast to the smooth perceived rotational velocity decay present in the majority of subjects, a sudden drop of perceived rotational velocity response occurred in about one third of our subjects. Could
the drop reflect a higher threshold of sensation in some subjects, i.e., could those subjects be more insensitive to sensory stimuli? The fact that the perceived rotational velocity curve before the drop was similar (including fit parameters) to that of the subjects without the drop makes the hypothesis of different sensation sensitivities unlikely. Interestingly, these subjects also showed a drop during the control trials with sound (for 2 typical examples, see Fig. B1 in APPENDIX B), whereas this was not the case in the subjects who did not show a drop during self-motion perception trials. Hence, we rather suggest that the drop behavior reflects a characteristic of sensorimotor transformation or a poorer manual motor performance. For example, one could postulate that the subjects with drops were less able to exploit the whole range of motor performance and thus stopped turning the lever at a higher lever spinning velocity but that their perception of angular velocity and sound was similar to the other subjects.

The main finding of this study was that slow-phase eye velocity and perceived rotational velocity responses to angular velocity steps could be accurately fitted using a weighted sum of the same two exponentials functions with different time constants: one accounting for the peripheral SCC dynamics and the other for the central velocity storage process. Differences between the curves of slow-phase eye velocity and sensation decay after earth-vertical angular velocity steps, Okada et al. (1999) recently hypothesized that a VSM, similar to the brain stem VSM for the rVOR, exists at perceptual, presumably cortical, level. Our results reinforce the hypothesis of a perceptual VSM. Because slow-phase eye velocity and perceived rotational velocity responses in our study, however, could accurately be fitted by exponential functions with the same peripheral and central time constants, we further suggest that the signals subserving self-motion perception and reflexive eye movement might be activated the same brain stem VSM.

Parameter estimations of central time constant in response to earth-vertical yaw rotations were in the range predicted for the rVOR in humans (10–30 s) (Büttner and Waepe 1981; Cohen et al. 1981; Dai et al. 1999; Fernandez and Goldberg 1971; Gizzi and Harper 2003; Hain and Zee 1992; Leigh and Zee 2006). During earth-vertical pitch rotations, however, parameter estimations of the central time constant were similar to those of the peripheral time constant. It is known that the vertical rVOR decays with a comparable time constant as its sensory (i.e., SCC) input, indicating relatively little, if any, velocity storage contribution (Balogh et al. 1983; Clément 2003; Hain and Zee 1992; Leigh and Zee 2006). Thus the question arises whether, in the vertical plane, slow-phase eye velocity traces could be accurately fitted with only a single exponential function with the peripheral time constant, whereas vertical perceived rotational velocity traces would require an additional central contribution to explain the plateau behavior. All fitted slow-phase eye velocity traces, however, had a nonzero VSM contribution, which provides evidence that the peripheral time constant that best fits both slow-phase eye velocity and perceived rotational velocity traces cannot explain the rVOR response on its own. We therefore conclude that our hypothesis of a common VSM contribution holds also for earth-vertical pitch rotations in both the rVOR and self-motion perception, although the VSM gain for the rVOR is weak.

Model interpretations

The equations used to fit slow-phase eye velocity and perceived rotational velocity responses represent the output of a modified version of the Raphan, Cohen, and Matsuo model (Raphan et al. 1977) and the Robinson model (Robinson 1977a) (see Introduction and Fig. 1, A and B). Because the two models rely on different hypotheses about the neural circuitry underlying the velocity storage process, two interpretations on how the VSM contributes to the rVOR and to self-motion perception can be given. We emphasize that, in the following arguments, we will not provide any interpretations on the functional purpose of the velocity storage network. Our aim instead is to show how rotational self-motion perception and reflexive eye movement responses to an angular velocity step can be viewed in the context of the two models and of a common velocity storage process. For a detailed description of both models, see APPENDIX A.

In our modified version of the Raphan, Cohen, and Matsuo model (Raphan et al. 1977), the rVOR and self-motion perception share the same central VSM process (Fig. 1A). The output of the VSM is fed into an indirect rVOR pathway and an indirect perceptual pathway, which are independently summed to their direct pathways. What characterizes the differences between slow-phase eye velocity and perceived rotational velocity within the same plane of rotation (i.e., yaw or pitch) are, according to our main conclusion, the gains along the direct and the indirect pathways. Differences in the responses to rotations in different planes (i.e., yaw and pitch) require instead 1) a lower time constant of the VSM, which affects both, the rVOR and self-motion perception, and 2) a reduced relative contribution of the indirect rVOR pathway during pitch rotations. Thus two concurrent modifications are needed for slow-phase eye velocity responses, whereas only one is needed for perceived rotational velocity responses, because the relative contribution of the indirect perceptual pathway is independent of the plane of rotation (i.e., no differences between \( R_{PRV} \) in yaw and pitch; see Table 1). Two possible hypotheses for explaining the differences between yaw and pitch rotations are plausible: 1) two separate central VSM processes for the horizontal and vertical plane of rotation with their respective time constants and gains or 2) a VSM structure with a shorter time constant and a smaller contribution to the indirect rVOR pathway during pitch rotations.

In the modified version of the Robinson model, in contrast, the perceptual VSM pathway stems from the feedback line, after the signal has been processed through the integrator element and is summed with an independent direct pathway from the periphery. This implies that the perception uses the information from the loop built around the rVOR pathway, or in other words, the feedback loop sets the appropriate rVOR behavior and sends a copy of its activity to the cortical perceptual level. As for the Raphan, Cohen, and Matsuo model, differences between slow-phase eye velocity and perceived
rotational velocity within the same rotation plane result from the gains along the direct and the indirect pathways. The differences between the Robinson and the Raphan, Cohen, and Matsuo models, however, emerge when reflexive eye movements and perceptual responses during rotations in different planes are studied. Specifically, when determining the parameters of the Robinson model from our results, we found that for both yaw and pitch rotations, the time constant of the leaky integrator ($\tau_L$) was similar as the peripheral (i.e., SCC) signal input (mean $\tau_L \pm SD$: 5.19 ± 1.74 s). Therefore $\tau_L$ was unchanged for rotations in different planes. What significantly differed between yaw and a pitch plane rotation was, however, the feedback gain parameter ($\beta_{\text{yaw}}$: mean $\beta \pm SD$: 0.64 ± 0.12; $\beta_{\text{pitch}}$: 0.3 ± 0.11). Compared with the Raphan, Cohen, and Matsuo model, which needs two concurrent modifications to explain the differences between yaw and pitch rotations, the Robinson model requires only a lower feedback loop gain ($\beta$) of the VSM when activated by the vertical semicircular canals.

In conclusion, our findings in healthy subjects suggest that rotary self-motion perception may receive signals from the same central processes as reflexive eye movements. The presence of neurons in the vestibular nuclei discharging in relation to changes in head orientation and not to eye movements (vestibular-only neurons) provides evidence that the computation of spatial orientation may take place as early as in the brain stem (Cullen and Roy 2004; Zhou et al. 2006). Of course, we do not preclude the possibility that self-motion perception can be further processed. As pointed out by others, reflexive eye movements and vestibular perception can be weakly correlated when using other motion stimuli, such as transient rotational motions, sinusoidal oscillations, tilts, and translations (Clément et al. 2008; Grunfeld et al. 2000; Guedry et al. 1992; Merfeld et al. 2005a,b; Park et al. 2006; Peterka and Benolken 1992; Wood et al. 2007). The fact that, in our experiment, self-motion perception paralleled the rVOR, however, shows that a further perceptual, possibly cortical, processing is not a necessary condition. The identification of shared mechanism between the rVOR and perception may have a key role in understanding how vestibular disorders affect self-motion perception, spatial orientation, and navigation.

## APPENDIX A: RELATION BETWEEN THE RAPHAN, COHEN, AND MATSUO AND THE ROBINSON MODEL

As outlined in the Introduction, two equivalent models explain the dynamics of the rVOR in response to a velocity step with two exponentials: the Raphan, Cohen, and Matsuo model (Raphan et al. 1977) and the Robinson model (Robinson 1977a). In the following, we present a description of the two models together with our modifications generating the perceptual output. We show how the response to a velocity step in our modified models is equivalent to Eq. 1 in METHODS. To distinguish the variables of the two models, the apex “C” will be used for the Raphan, Cohen, and Matsuo model and “R” for the Robinson model.

### Raphan, Cohen, and Matsuo model

The Raphan, Cohen, and Matsuo model hypothesizes that the rVOR results from an indirect pathway that parallels a direct pathway responsible for carrying the SCC afferent signal directly to the ocular motor neurons (3-neuron arc). The VSM is implemented along the indirect pathway with an independent time constant ($\tau_{\text{VSM}}$) on its own (Raphan et al. 1977). Each pathway is weighted by its own gain. For a graphical representation of the model, see Fig. 1A in the Introduction. According to Fig. 1A, the I/O (input–output) relation of the model in Laplace form, can be written as

\[
\begin{align*}
O &= s g \frac{s \tau_C}{s \tau_C + 1} I + s g \frac{s \tau_C}{s \tau_C + 1} X \\
X &= \frac{s \tau_C}{s \tau_C + 1} I - \frac{s \tau_C}{s \tau_C + 1} X \frac{s \tau_{\text{VSM}}}{s \tau_{\text{VSM}} + 1} \frac{s \tau_{\text{VSM}}}{s \tau_{\text{VSM}} + 1} I \\
\end{align*}
\]

(A1)

where $s$ is the Laplace variable, $X$ is the internal state variable representing the output of the VSM, $g_D$ and $g_C$ are the direct and indirect pathway gains, respectively, and $\tau_C$ and $\tau_{\text{VSM}}$ are the SCC and VSM time constants, respectively.

In the time domain, the slow-phase eye velocity response to a unit step of head velocity predicted by the Raphan, Cohen, and Matsuo model is the inverse transform of the I/O equation in Eq. A1 multiplied by 1/s and is expressed by the following equation

\[
\dot{\theta}_C = g_D e^{-\frac{s \tau_C}{\tau_C} \theta_C} + g_I \frac{s \tau_{\text{VSM}}}{s \tau_{\text{VSM}} + 1} e^{-\frac{s \tau_{\text{VSM}}}{\tau_{\text{VSM}}} \theta_{\text{VSM}}} \]

(A2)

In our modified version of this model, self-motion perception and the rVOR share the same central VSM process (see Fig. 1A). The output of the VSM is divided into an indirect rVOR pathway and an indirect perceptual pathway, which are independently summed to their direct pathways. Thus the model output is made of two equations, one for slow-phase eye velocity ($\dot{\theta}_C$) and one for perceived rotational velocity ($\dot{\theta}_\text{perception}$), which share the same SCC and VSM time constants but are independent in their gains
Robinson model

In the Robinson model, the VSM is implemented via a feedback loop along the direct rVOR pathway (Robinson 1977a). Within the feedback loop a gain parameter ($\beta$) and a leaky integrator element

\[
\begin{align*}
O &= g_R \frac{s \tau_C^R}{s \tau_C^R + 1} I + X^R \\
X^R &= \frac{\beta R}{s \tau_L^R + 1} \left( \frac{s \tau_C^R}{s \tau_C^R + 1} I + X^R \right)
\end{align*}
\]

where $\tau_C^R$ and $\tau_L^R$ are the time constants of the SCC and of the leaky integrator, whereas $\beta R$ and $g_R^L$ are the gains on the feedback line and of the rVOR, respectively.

In the time domain, the slow-phase eye velocity response to a unit step of head velocity predicted by the Robinson model is the inverse of the rVOR, respectively.

Expressed by the following equation

\[
\dot{\theta}^R = \frac{\beta}{s \tau_C^R} e^{-\frac{\tau_C^R}{\tau_L^R}} I + \frac{\beta}{s \tau_C^R} \left( e^{-\frac{\tau_C^R}{\tau_L^R} - \frac{\tau_C^R}{s \tau_C^R + 1} I} \right)
\]

In our modified model version, we hypothesize that the perceptual VSM pathway stems from the feedback line, after the signal has being processed thought the integrator element, and is summed with an independent direct pathway from the periphery. Our assumption about the pathways providing the perceptual output is based on a previous study, suggesting the same structures in a model for vestibular nystagmus evoked by active head rotations in darkness (Ramat et al. 2003). The two equations generated by our modified model for slow-phase eye velocity ($\dot{\theta}_{\text{eye}}^R$) and for perceived rotational velocity ($\dot{\theta}_{\text{perception}}^R$) share the same SCC ($\tau_C^R$) and integrator ($\tau_L^R$) time constants, as well as the gain of the feedback loop ($\beta R$), whereas the gains of perceived rotational velocity from the SCC ($g_{D_{\text{perception}}}^R$) and from the VSM loop ($g_{I_{\text{perception}}}^R$) are independent

\[
\begin{align*}
\dot{\theta}_{\text{eye}}^R &= \frac{\beta}{s \tau_C^R} e^{-\frac{\tau_C^R}{\tau_L^R}} I + \frac{\beta}{s \tau_C^R} \left( e^{-\frac{\tau_C^R}{\tau_L^R} - \frac{\tau_C^R}{s \tau_C^R + 1} I} \right) \\
\dot{\theta}_{\text{perception}}^R &= \frac{\beta}{s \tau_C^R} e^{-\frac{\tau_C^R}{\tau_L^R}} I + \frac{\beta}{s \tau_C^R} \left( e^{-\frac{\tau_C^R}{\tau_L^R} - \frac{\tau_C^R}{s \tau_C^R + 1} I} \right)
\end{align*}
\]

FIG. B1. Example of sound used for the motor testing as recorded by microphone (top), perceived sound (middle) as reported by lever turning (dotted line: sound decay recorded by microphone for comparison), and mean of PRV traces as reported by lever turning during earth-vertical yaw rotations (bottom) in 2 subjects. The sound decayed exponentially in both loudness and frequency. Note that this sound decay does not equal an exponential decrease in hearing, because equal loudness curves are nonlinear in the frequency domain. However, the sound loudness and frequency function was selected because it was clearly perceived as a decaying sound by 3 investigators (G.B., S.M., A.P.) compared with a sound decreasing only in loudness and a sound decreasing only in frequency, a.u., arbitrary units.
In conclusion, both models with specific substitution of their variables generate the same set of equations for the response to a velocity step (Eq. 1) and thus are mathematically indistinguishable.

Note that Eq. 1 uses six parameters with 4 df to fit the differences between slow-phase eye velocity and perceived rotational velocity, because the two time constants \( \tau_c \) and \( \tau_{VSM} \) were constraint. One parameter of each equation, however, is a scaling factor, and therefore does not account for the differences in the dynamics of the two (slow-phase eye velocity and perceived rotational velocity) traces. As a conclusion, only 2 df are used to fit the differences in slow-phase eye velocity and perceived rotational velocity dynamics, whereas the other two represent the scaling factors.

**APPENDIX B: CONTROL TRIALS WITH ACUSTIC SIMULATION**

To study whether differences between rotational self-motion perception and the rotational vestibulo-ocular reflex were primarily caused by technical or skeleto-motor limitations of the lever spinning, the following testing trial was applied in each subject before the vestibular experiments: subjects, already seated in the nonmoving turntable, were exposed to a sound that was decreasing in amplitude and frequency along an exponential function (Fig. B1, top row). They were asked to match the decrease of the decaying sound by turning the lever. Visual inspection of the lever spinning traces recorded during the sound decay was used to assess the motor performance of each subject. In all subjects participating in this study, perceived sound decayed over time roughly following the recorded sound behavior. Results from two typical subjects are shown in Fig. B1 (A.S., left column; J.M., right column; lever turning: middle row, solid lines; sound decay as recorded by microphone: middle row, dotted lines).

Results from the perceived sound decay were, in addition, used to investigate the nature of two features observed in perceived rotational velocity curves recorded during turntable rotations: the plateau in the beginning and the drop in the last part of the perceived rotational velocity traces. Note the lack of a plateau in the sound contrasting the presence of a plateau in the vestibular traces in the two typical subjects shown in Fig. B1 (perceived sound: middle row; perceived rotational velocity: bottom row), suggesting that the plateau phenomenon is related to the kind of sensory stimulus evoking the perception and not to a technical or skeleto-motor artifact. On the other hand, subject A.S. (left) shows a drop (defined as a sudden stop of lever turning at a velocity >20% of the maximal velocity, see Data analysis and Fig. 4) for both sound perception and perceived rotational velocity, whereas in subject J.M. (right), no drop is observed in both sound and vestibular trials, suggesting that the drop is a specific characteristic of the way the subjects reports the perception trough the lever, i.e., a motor or artifact.

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**DISCLOSURES**

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