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Geometrical considerations on canal-otolith interactions during OVAR and Bayesian modelling

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During constant-velocity rotation about a tilted axis (OVAR), the VOR and the rotation perception last indefinitely, but show a striking dependency on tilt angle. We show that, during OVAR, a variety of motions can account for the head motion relative to gravity. Some of these are in conflict with canal signals, but correspond to a lower angular velocity; we suggest that the brain performs a trade-off in order to select the best motion. We show that this theory explains the effect of tilt angle on velocity estimation during OVAR.

Introduction

During a constant velocity rotation about an axis tilted with respect to gravity (also called Off Vertical Axis Rotation, OVAR), the angular velocity signal originating from the canals decays away. However, the orientation of the head relative to gravity changes constantly, which has been shown to give rise to a continuous perception of rotation, provided that the tilt angle is large enough (Guedry, 1965). Previous modelling work has proposed that the brain constructs an estimate of motion in space from otolith signals, which matches sensory signals (Bos and Bles, 2002). During OVAR, a sustained estimate of rotation can account for head reorientation relative to gravity, and is therefore coherent with sensory signals. Nonetheless, modelling motion perception and vestibulo-ocular reflexes during OVAR remains a challenging task, mainly due to the complexity of the tri-dimensional motion and the multiplicity of sensory sources involved.

In the present report, we show how to simplify the problem of angular motion estimation during OVAR, assuming that the head orientation is perceived correctly. Specifically, we point out and formalize two aspects of motion estimation during OVAR: (1) that there is a variety of head motions that lead to the same otolith stimulation as during OVAR and (2) that the information provided by the semicircular canals plays a role in the estimation process.

Otolith signals

During OVAR, the angular velocity of the head can be represented by a vector Ω_0, which is aligned with head-fixed Z axis (see Fig. 1a). In an egocentric frame of reference, this rotation causes the gravity vector G to rotate around Z, according to $G' = - \Omega_0 \times G$, where G' is the time derivative of G and 'x' represents the vector cross product (see Fig. 1b). A fundamental observation is that any angular velocity vector Ω who satisfies the equation $G' = - \Omega \times G$ (i.e. $\Omega \times G = \Omega_0 \times G$) can explain the displacement of G, and is therefore coherent with the otolithic input (also see Hess, 1992). The ensemble of possible Ω vectors is simple to compute. If we decompose Ω as the sum of Ω_0 and an additional vector Ω_1 (i.e. $\Omega = \Omega_0 + \Omega_1$), we obtain $(\Omega_0 + \Omega_1) \times G = \Omega_0 \times G$ i.e. $\Omega_1 \times G = 0$. This means that the additional velocity vector has to be parallel to G. The ensemble of possible velocity vectors is represented on Fig 1.b as a line λ (which passes at Ω_0 and is parallel to G).

Another observation is that some velocity vectors have a smaller magnitude than Ω, which means that they correspond to a smaller angular velocity. The vector with the smallest magnitude is $\Omega_m = - G \times G' / |G|^2$. We previously presented the hypothesis that the brain favours motion estimates with a lower angular velocity (Laurens and Droulez, 2007). Accordingly, we would expect that, on the basis of otolith signal only, the perceived motion corresponds to Ω_m.

*** Insert Fig.1 here ***

Semicircular canal signals

In a steady state, Ω_0 does not vary over time in an egocentric frame of reference. It corresponds to a constant-velocity rotation about the head vertical axis, which is only detected at the beginning of rotation by the semicircular canals. This peripheral input typically fades away over a few seconds. In contrast, the other angular velocity vectors continuously rotate around Z. For instance, the trajectory of the Ω_m vector is illustrated in Fig. 1c. The projection of Ω_m on the Z axis is constant, whereas its projection on the (X,Y) plane is rotating around the origin. Therefore, the projection on the X and Y axis varies sinusoidally over time (Fig. 1c). In other words, Ω_m correspond to the summation of a constant-velocity rotation in yaw and of pitch and roll oscillations (as illustrated on Fig. 1d). In terms of sensory inputs, a motion corresponding to the vector Ω_m would not activate the horizontal canals, but the dynamic pitch and roll components would activate the vertical canals. As these canals are not activated during the real OVAR, the motion corresponding to Ω_m is in conflict with their signal. For a given vector Ω, this conflict is proportional to the amplitude of the pitch and roll oscillations, which is represented by the projection of Ω on the X,Y plane. As pitch and roll oscillations are equivalent for the purpose of our demonstration, the Fig. 1c can be reduced to a two dimensional diagram (Fig. 1e), in which the abscissa represents the amplitude of the pitch and roll oscillations, and the ordinate the constant yaw velocity component.

This diagram allows capturing the issues discussed above in a simple geometrical representation. The ensemble of possible motions forms a line λ, passing through the Ω vector with an angle α relative to the ordinate. The Ω_m vector is obtained by orthogonal projection of the origin on line λ. Each possible motion is represented by a vector Ω. The length of Ω is equal to the angular velocity of this possible motion, and its projection on the abscissa represents the magnitude of the conflict with the vertical canals.

*** Insert Fig. 2 here ***

Bayesian modelling

In a previous work, we implemented a general Bayesian model of self-motion perception (Laurens and Droulez, 2007), as well as a simplified model dedicated to motion estimation during OVAR (Laurens, 2006). The latter uses the constraints described above. We will briefly describe the principles of this estimation by using the diagram in Fig. 2a. The model assumes that motion perception during OVAR can be modelled as a trade-off between the minimization of the angular velocity and the minimization of the conflict with canals signal. Therefore the perceived motion (Ω_f) is expected to fall between the vectors Ω_m (which minimizes the angular velocity) and the vector Ω_0 (for which there is no conflict). This trade-off can easily be visualised for two angles of tilt on the Fig. 2b,c. For a small angle of tilt ($\alpha = 15°$, Fig 2.b), the vector Ω_m has a very small magnitude compared to Ω_0. Furthermore, its projection on the abscissa is small, which means that it corresponds to a small conflict. Therefore the optimal motion is Ω_m. This explains the absence of yaw rotation perception at small angles of tilt (Denise et al.,1988; Vingoerhoets et al., 2006). In contrast, for a tilt angle of 45° (Fig 2.c), Ω_m has a higher yaw component. As it also corresponds to a higher conflict, Ω_f falls between Ω_m and Ω_0. As the tilt angle approaches 90°, Ω_f gets closer to Ω_0. This explains the close to veridical motion perception during OVAR with a large angle of tilt (Guedry, 1965).

Conclusion

It is widely accepted that the brain can derive an angular velocity estimate from the otolith input during OVAR. We have formalized this process and shown that a variety of motion is compatible with the otolith signal. We also emphasize the role of the information provided by the canals during OVAR. In particular, we demonstrate that, although this signal fades away during OVAR, it contributes to deducing that the head is rotating at a constant velocity.

Acknowledgements

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List of Abbreviations

OVAR: Off-Vertical Axis Rotation; VOR: Vestibulo-Ocular Reflex

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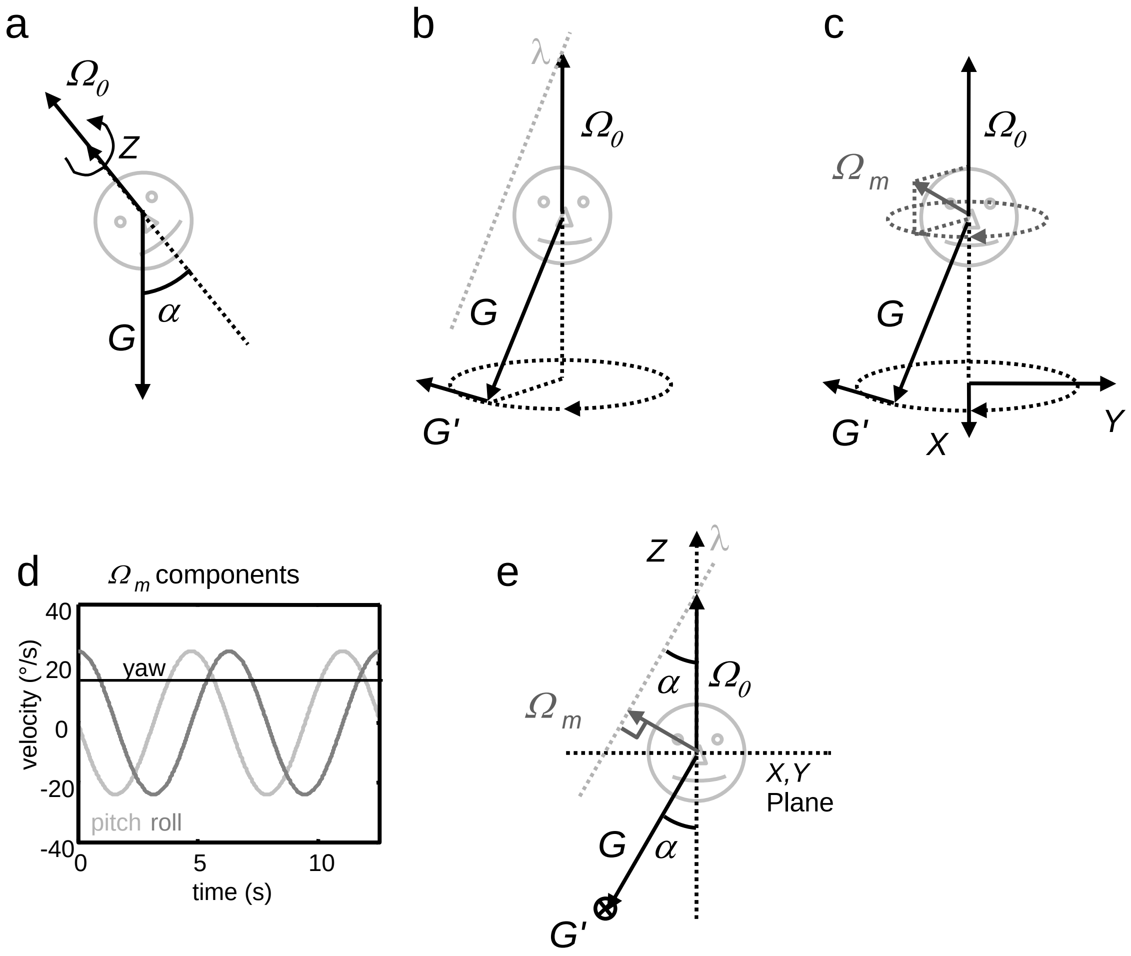
Figure legends:

Figure 1: Geometrical aspects of OVAR. a: motion of the head in a geocentric reference frame. b: displacement of gravity (G) in an egocentric reference frame, and ensemble of possible rotation vectors. c: motion of the vector Ω_m relative to the head. d: instantaneous

head velocity corresponding to Ω_m. e: reformulation of the diagrams b and c in two dimensions.

Figure 2: Optimal estimation of motion in a general case (a), for tilt angles of 15° (b) and 45° (c). See text for details.


a
Ω0
Z
α
G
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c
Ω0
Ωm
G
G′
X
Y
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Ωm components
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20
0
-20
-40
velocity (°/s)
yaw
pitch
roll
0
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time (s)
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Figure 1

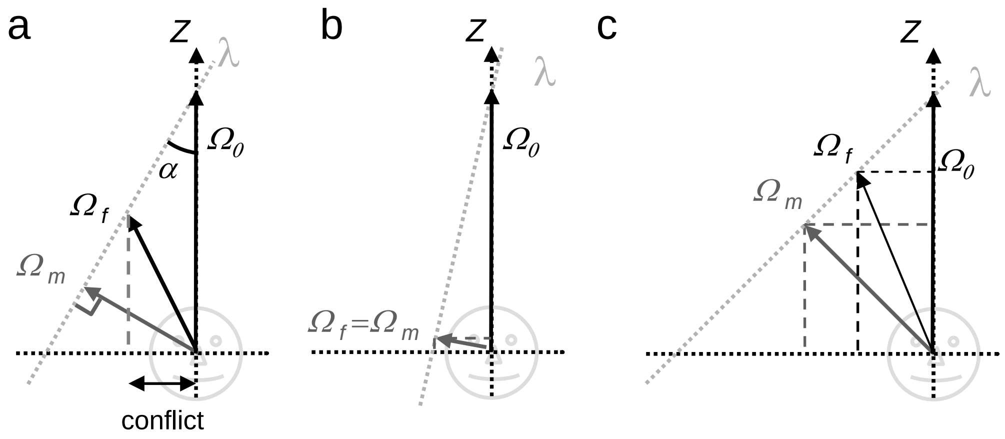

Figure 2