

Non-linear Galilean Vestibular Receptive Fields

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Abstract—We present a set of formulas for the receptive fields of the vestibular neurons that are motivated by Galilean invariance. We show that these formulas explain non-trivial data in neurophysiology, and suggest new hypothesis to be tested in dynamical 3D conditions. Moreover our model offers a way for neuronal computing with 3D displacements, which is reputed to be hard, underlying the vestibular reflexes. This computation is presented in a Bayesian framework. The basis of the model is the necessity of living bodies to work invariantly in space-time, allied to the necessary discreteness of neuronal transmission.

Many studies on the vestibular system have insisted on the necessity to take in account the 3D+1 aspects of the vestibular integration, as well as its essential multi-sensory functioning., cf. [2], [3]. However the complexity of responses in the vestibular centers of the brain and the difficulty of 3D natural stimulations make difficult the understanding of vestibular neuronal activity. Responses of vestibular neurons were first described by Adrian, then by Shimazu and Precht, see Wilson and Melvill Jones [1], and more recent experiments have considerably augmented our knowledge of these activities ([2,3,4,5,6,7]). Epithelia of end organs in the inner ear, semi-circular canals cristae and otoliths maculae, have overlapping projection in the vestibular nuclei and the cerebellum [3], where they generate tonic or phasic kinetic activities, able to differentiate between active or passive head movements (Cullen-Roy [13]), or between movements of head alone, of trunk alone or of both together (Marlinski, McCrea [9]). A linear formula in the stimuli vectors explains a part of the responses in 2D conditions, but the 3D aspects are still obscure (cf. [4]). Most neurons in the vestibular nuclei, or the vestibular cerebellum (flocculus, uvula, nodulus, paraflocculus) and the fastigial nucleus, for instance, are also strongly modulated by the visual system (eye position or vision), by proprioception, and by many other inputs, from the skin and muscles of the limbs and trunk as well as viscera [14].

The aim of the present communication is to propose a hypothesis for the forms of the possible elementary responses of the vestibular neurons, based on Galilean invariance, extending the manner that primary cortical visual receptive fields are based on Fourier analysis or wavelets. This gives a conjectural set of possible receptive fields

(RFs). Some of them correspond to known observations, putting mathematical order on the data, but other ones offer new suggestions to be tested.

It seems *a priori* difficult for the vestibular neurons to reconstitute a complete Galilean invariance, as physicists have discovered it in empty space, because the gravity breaks the Galilean symmetry in general. However, it is known that the population of vestibular neurons is able to separate the gravity from the linear acceleration (Angelaki et al. [16]), and that human subjects behave as if they possess internal models of the fundamental laws of the Mechanics (Merfeld et al. [10], McIntyre et al. [11], Indovina et al. [12]). Thus we suggest that the system is able to coherently treat gravity plus acceleration, preserving Galilean relativity. This is conform with the discovery of Yashukeva et al. [5], that the vestibular neurons in the posterior cerebellar vermis are working in inertial frames.

I. THE NOTION OF INVARIANT RECEPTIVE FIELD

Let us follow the information flow from the vestibular end organs to the vestibular nuclei (VN) and cerebellum, then to the thalamus and to the cortex or cerebellum and back to VN. The cupula membrane in the ampulla of semi-circular canals reacts to angular accelerations of the head in space, but, due to the biophysic of the endolymph and of the cupula, the signals regress to angular velocity. The otoliths react to the linear acceleration of the head and to the gravitation, then the signal is transmitted to the vestibular nerve. This is the right order for Galilean relativity, because this implies that semi-circular and otoliths signals together define a tangent vector to the linear part of the Galilée group, a 6 dimensional velocity. Note that the physiology of the cristae afferent neurons permits to reconstitute in part an angular acceleration signal, this is the role of the irregular phasic subsystem, but on the side of otoliths, the linear jerk is partly transmitted accordingly, again saving relativity. See [14].

In the Nodulus and Uvula (respectively lobules 10 and 9 of caudal posterior vermis) of monkeys, Jakusheva et al. [5] established that the complex spikes (CS) of Purkinje cells contain information on the linear acceleration of the head and its angular velocity. Most central vestibular neurons are modulated by vision and other sensory inputs; we pretend that this again is compatible with relativity inside the brain, because inertial changes, as translation, or rotation, cannot be detected by vestibular end organs only, so the Galilean invariance needs other inputs like visual input, to be complete. In this respect it is worth mentioning that the accessory optic system (MTN, DTN, LTN), where neurons respond to large moving visual stimuli, and are involved in

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eye movements control, in strong interaction with the pretectal NOT and the Inferior Olive, is also organized in the planes of the semicircular canals.

We want to explore the consequences of the following observations of Helmholtz and Poincaré, that the access of living entities to space and time needs movements and the notion of invariance. The theory of groups in Mathematics was invented to formalize invariance, symmetry and ambiguity. The theory of Relativity in Physics is the ancestor of this program. On another side, space and time are not given first in usual terms of position and date, but they are accessible only through frequency and impulsion data.

Invariance is coded in a certain *group*, which is a set of transformations, acting on a space, and which is stable by compositions and inversions. In our situation the Galilée group of the relativity of motion in classical Physics is dominant (but not exclusive). The theory of group invariants has a modern formulation, named *harmonic analysis*, where we consider all the matrix (*a priori* infinite) representations of the group that are unitary (for compatibility with probability) and irreducible (for elementary decomposition). This theory is fundamental for today Chemistry and Quantum Physics. Our hypothesis is that neurons associated to a certain group transform the signal they receive according to certain coefficients of matrices in such representations. To understand the origin of this hypothesis, note that space-time is defined by a kind of invariance (depending on context), thus a coherent action must be prepared first in invariant terms. Then it comes a computational reason: the discrete functioning of neurons must be compatible with the mentioned invariance. And working in the dual world of coefficients of representations is a solution.

This hypothesis is an occurrence of the composite variables [18]. We show in section III how it relates to Bayes analysis.

Let us describe with more details the notion of invariant receptive fields. In the case of the visual cortex we are familiar with the model (NLL) formula, which gives the probability of responses of a cell in function of the image stimulus as a linear operator, with kernel K , followed by a static non-linearity in sigmoidal form σ . For each simple subunit a_0 the formula for the probability of modulation of response at time t for the moving image is

$$R(t) = \sigma[Re(\widehat{K}\widehat{I}_t(\xi_0, \eta_0, \omega_0)e^{i\varphi_0})]$$

where the hat symbol denotes the Fourier transform and the index t denotes a delay by t . The letters $\xi_0, \eta_0, \omega_0, \varphi_0$ denote the preferred frequencies (spatial and temporal) and the preferred phase, respectively, cf. [19]. Thus precisely

$$R(t) = \sigma(Re(\int \int \int K_0(x-x_0, y-y_0, s-s_0) I(x, y, t-s) e^{-i(x\xi_0 + y\eta_0 + s\omega_0 + \varphi)} dx dy ds))$$

This classical formula is nothing else that commutative harmonic analysis, it describes how the signal is captured in frequency terms in a space-time windows. This corresponds to the fact that the translations group (in visual plane here) being commutative, its irreducible representations are one-dimensional, which is no longer true for the displacements group or in the case of Galilean invariance. Note that the reality of the frequency vector guaranties the unitarity.

Remark: the interpretation of the response formulas by harmonic analysis comes from Gabor, cf. [20]. Several Lie groups were considered in vision theory, for instance the Heisenberg group (Kalisa, Torresani [26]), the plane displacements $E(2)$, (Sarti et al. [25], Bressloff et al. [27]), the plane hyperbolic group (Chossat and Faugeras [24]). In all these studies the wavelet aspect is fundamental. It is known that wavelets have much to do with information theory.

II. THE GALILEAN INVARIANCE

The Galilée group G acts on the four dimensional space-time $R^3 \times R$. Imagine a frame, made by an origin in this space-time, and by four vectors, three in space and one in time (pointing to the future). The full group G is formed by products of instantaneous translations of the origin in space-time (four parameters), of rotations (three parameters) and of constant velocity translations or gliding:

$$\vec{X} = \vec{x} - \vec{a}t \quad ; \quad T = t.$$

The subgroup generated by rotations and gliding only is called the linear group G_0 . This is the subgroup sensed by the vestibular end organs, through infinitesimal variation.

The first ingredient of a receptive field for a cell c is a pair (σ_c, K_c) of one sigmoidal real function of one real variable and one real smooth function on $G \times R$, such that the activity of c at time t induced by a distribution $\mu(t)$ of movements stimuli is given by the formula

$$R_t(\mu) = \sigma_c[K_c * (\tau_t \mu)^V].$$

(In general $\mu(t)$ is concentrated on a given element in G .)

Our suggestion is that K_c is given by a coefficient in an irreducible unitary representation of G , for maximizing invariance and information together.

The unitary representations of G or G_0 were determined by Ito and Mackey in the fifties. Cf. [22].

Example, in the case of G_0 we choose a real number ρ , the Hilbert space H of the linear representation is the space of square integrable functions on the 2-dimensional sphere, if g is the product of a rotation R and a gliding of velocity vector \vec{a} , we have the following formula

$$U^\rho(g)(f)(\vec{x}) = e^{i\rho\vec{a}\cdot\vec{x}} f(R^{-1}\vec{x})$$

The standard coefficients in this case are associated to the basis of H made by spherical harmonic functions $P_{l,k}$, cf. [21]. In the simplest cases, where one of the basis vector is a constant polynomial, the unitary coefficients do not depend on the rotation R , and they are equals to products of one polynomial in the coordinates of the direction α of the velocity \vec{a} with a Bessel function of the product of ρ with the norm r of \vec{a} . This gives formulas well adapted to describe the gravito-inertial only cells. The structure of these coefficients can explain the phenomenon discovered by Angelaki et al. [4] of a non-zero response with advanced phase $\pi/2$, that are elicited along the direction orthogonal to the direction of maximal sensitivity. In fact we have

$$P_{l,k}(x, y, z) = A_{l,k} r^{l-k} C_{l-k}^{k+1/2}(z/r)(x \pm iy)^k$$

where C_{l-k} denotes a Gegenbauer polynomial, for instance

$$C_1^p(z) = pz, \quad C_2^p(z) = 2p(p+1)\left(z^2 - \frac{1}{2p+2}\right),$$

thus, for $l=2, k=1$, for instance, we get for the coefficient a dependence in the norm r , a principal dependence in the z direction, but also a secondary dependence in the transverse plane x, y with an imaginary coefficient, that generates a phase difference in this direction for the receptive field after taking the real part, and applying the non-linearity.

Let us describe the general formula of the RFs: we choose a standard function $K_0(t)$ on the group G , like a Gaussian, centred on the identity element of G , explicitly dependent on time t , we also choose an irreducible unitary representation $\lambda(t)$, in general dependent on t , and two vectors $\psi_1(t), \psi_2(t)$ in the Hilbert space H of the representation $\lambda(t)$. Then the proposed formula is

$$K_c * (\tau_t \mu)^\vee = \int_{\mathbb{R}} ds \int_G dh K_0(g_0 h^{-1}, s) (\psi_1(s) | U^{\lambda(s)}(g_0 h^{-1}) | \psi_2(s)) \mu(h, t-s)$$

integrating the product of an unitary coefficient with the decentred Gaussian, that is a time dependent wavelet for the group G .

The representation $\lambda(t)$ plays the role of the preferred frequency, while $K_0(t)$ is the spatial envelop of a Gabor wavelet, giving the size to the window the neuron has on the world. The vectors $\psi_1(t), \psi_2(t)$ play the role of a phase,

they are necessary when G is non-abelian, so they are new elements with respect to the abelian case of visual cells.

Remark: in the simplified case of 2D analysis, the response to a stimulus of frequency ω in a direction θ is given by:

$$R(t) = \int k_0(s) ds \cos(m(\theta - \theta_0)) J_m(\rho_0 \cos(\omega(t-s)))$$

where J_m is the Bessel function of order m .

At first order approximation in the constant ρ_0 this gives:

$$R(t) = \rho_0 \int k_0(s) ds \cos(m(\theta - \theta_0)) \cos(\omega(t-s)).$$

And when the kernel k_0 is of Dirac type $\delta(t-t_0)$, we find the classical model:

$$R(t) = \rho_0 \cos(m(\theta - \theta_0)) \cos(\omega(t-t_0)).$$

However, when k_0 is a real Riemann-Liouville derivative of real order D_0 , we find a "dynamical response":

$$R(t) = \rho_0 \omega^{D_0} \cos(m(\theta - \theta_0)) \cos(\omega(t-t'_0)).$$

This response is typical of a vestibular kinetic neuron. The usual characteristics are thus the gain ρ_0 , the phase delay t'_0 and the dynamical index D_0 .

An important property, for the information decomposition, is the orthogonality of the unitary coefficients. When the group G is compact, commutative or not, the Schur and Weyl theorems affirm that a natural orthogonal basis of the algebra of functions on G is formed by the coefficients of the set of non-isomorphic irreducible unitary representations of G , i.e. the group applications from G to any complex unitary group $U(n)$ of complex $n \times n$ matrices M , verifying $M^* M = \text{Id}$. However the groups that are the most interesting for us are not compact Lie groups, except for rotation only cells, which exist but represent a small percentage of cells. The interesting irreducible unitary representations of these groups are infinite dimensional. But for the Galilée group G , the theorem also holds: the coefficients of the unitary irreducible representations form a generating system of the functions on G , this is the content of the Plancherel formula, and these coefficients have also strong orthogonality properties (Harish-Chandra, cf. [22]), making them well adapted for information decomposition.

III. BAYESIAN COMPUTATIONS

The Bayes theorem gives a linear recurrence relation in time for the subjective probability U_t (for convenience we

will use non-normalized probabilities i.e. finite measures) of an external world variable ξ_t or a desired action α_t . The coefficients of the relation are the ratios of an activation probability by an *a priori* probability on ξ_t or α_t (Laurens-Droulez, [17], Angelaki et al. [15]). In our case, we can consider the external stimulus as a transition between frames in the group of Galilée, from an element g to an element h , given a sequence of vestibular activities $S(0), \dots, S(t)$. If we denote by ω the noise in vestibular transduction, then the recurrence relation can be written:

$$U_t(g; \omega) = \sum R_t(S(t), S(t-1), \dots, [g, h; \omega]) U_{t-1}(h; \omega)$$

The letter S represents the collection of state variables of the N neurons of the CNS that are involved: S_0, S_1, \dots, S_N , then R_t is a joined probability of N random variables.

Now we propose to replace the sum over h in the group G by a continuous integral, this corresponds to view neurons as working in the dual space \hat{G} of representation's coefficients.

If the invariance is perfect, $R_t(S | g, h, \omega)$ only depends on the ratio gh^{-1} in G . In this case we obtain what is called a convolution operator. The theory of linear representation tells us that after a generalized Fourier-Plancherel transform this convolution is replaced by a matrix multiplication system. This fits well with the observation that often the cortical neurons are disposed in sub-populations corresponding to the same generalized frequency. That is suspected to simplify the computation. Our model suggests in what sense the simplification is achieved: this is to represent matrices by connections. It appears also that the neurons are numerous for invariant computation.

Because the coefficients of unitary representations are oscillatory operators, the CNS has to work with adapted oscillations, in a dual world, as advocated by R.Llinas [23]. The reflected properties of space-time in the neuronal operators are totally transformed, in this dual world of coefficients, but the space-time invariance is preserved.

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