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Three Dimensional Frames of Reference Transformations using Gain Modulated Populations of Neurons

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Abstract. This work investigates whether population vector coding could be a principle mechanism for sensorimotor transformations. This paper presents a formal demonstration of how population vector coding can proceed arbitrary 3-dimensional rotations and translations. The model suggests that population coding could be a possible mechanism for frames of reference transformations across multiple sensori-motor systems.

1 Introduction

When performing visually-guided movements, the brain faces the task of transferring information across different frames of reference. Visual information gathered in a retina-based frame of reference (FR) must be transferred first in head-centered FR, then in body-centered FR, and finally in hand-centered FR. In this paper, we investigate how population vector coding can be used as a principle mechanism to accomplish FR transformations.

Population vector coding is a computational paradigm shared by several areas of the nervous system, including proprioceptive receptors, such as muscle spindles [5], the motor cortex [10], and parts of the sensorimotor pathway, such as the posterior parietal cortex [9]. Population vector coding appears, thus, to be a common principle of brain organization, through which different neural populations interact and share information in the purpose of accomplishing tasks, by integrating multimodal informations for distributed control across the whole body.

We present a formal demonstration of how population vector coding can proceed arbitrary 3-dimensional (3D) rotations and translations. Other works [1, 2, 6] investigating FR transformations using population vector coding, considered implicitly that some neurons produced a multiplicative response of their inputs. In contrast, our approach derives the multiplicative property of the population output from the concurrent activity of a population of integrative neurons. Integrative properties of neurons are in line with a biological account of neural response.

2 Population Vector Coding

Each neuron participating in the population vector code is characterized by three major properties: 1) a *preferred direction* (PD), i.e. the direction for which its firing rate is maximal, 2) a *cosine tuning curve* [10], i.e. the neural activity is modulated proportionally to the dot product between the direction coded by the population and its preferred direction; 3) *gain modulation* [3], i.e. the neural activity can be modulated multiplicatively by a constant external input. Gain modulation and cosine tuning curve result from lateral inhibitory and excitatory connections within the population. The population's dynamics is characterised by in *attractor networks* [7, 11].

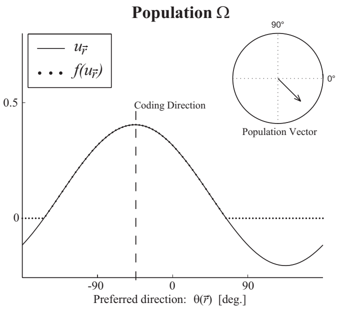

Figure 1: Population vector (top right), and neural activity of a 2 dimensional population, where units are sorted by their preferred direction $\vec{r} = (\cos(\theta), \sin(\theta))$.

Let Ω be a continuous population of neurons, where each unit is referred to by its preferred direction $\vec{r}$, uniformly distributed along a two or three dimensional subspace defined by $\Gamma^N = \{\vec{r} \in \mathbb{R}^N \mid \|\vec{r}\| = 1\}$, $N = \{2, 3\}$, respectively. Let $u_{\vec{r}}$ be the membrane potential of the neuron with PD $\vec{r}$, and $f(u_{\vec{r}})$ its firing activity. f is a non-linear function equals to $f(x) = [x]^+$, i.e. it returns the positive part of the input. Each neuron fires preferentially for its PD. The neuron's potential is modeled by

$$u_{\vec{r}} = \alpha + \beta \ (\vec{r} \cdot \vec{r}_v), \tag{1}$$

where α is the baseline firing rate and β the cosine amplitude. By construction, for $\alpha = 0$, the population as a whole fires maximally for the direction represented by the vector $\vec{r}_v$ with an amplitude proportional to β, (see fig. 1). In other words, the population can be tuned to encode an arbitrary vector $\vec{v} = \beta_v \vec{r}_v$[1] by setting the activity of all neurons in the population to $u_{\vec{r}} = \beta_v \ (\vec{r} \cdot \vec{r}_v)$.

3 Attractor Network and Gain Modulation

Consider now a fully connected population Ω_R, whose dynamics is governed by

$$\tau \dot{u}_{\vec{r}} = -u_{\vec{r}} + \oint_{\Gamma} w^{R \to R}_{\vec{r}' \to \vec{r}} f(u_{\vec{r}'}) \, \mathrm{d}\vec{r}' + x_{\vec{r}} \qquad w^{R \to R}_{\vec{r}' \to \vec{r}} = \gamma \, (\vec{r} \cdot \vec{r}'), \tag{2}$$

where $w^{R \to R}$ correspond to the lateral connections across neurons within the same population. The lateral connections exhibit symmetric, rotation invariant, and center-surround excitation-inhibition characteristics. $x_{\vec{r}}$ is the sum of all external synaptic inputs and γ is a constant scaling factor (see table 1). In the rest of the paper, we will restrict our study on inputs having the form:

$$x_{\vec{r}} = h + \beta_{v_0} \ (\vec{r} \cdot \vec{r}_{v_0}). \tag{3}$$

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[1] where $\|\vec{r}_v\| = 1$ and $\beta_v = \|\vec{v}\|$

Let us first consider the case in which the input is constant across the whole network $x_{\vec{r}} = h$. We can show that the network will converge to a stable attractor state, given by:

$$u_{\vec{r}} = \begin{cases} h\left(1 + \frac{1}{\eta}\left(\vec{r} \cdot \vec{r}_v\right)\right) & h > 0 \\ h & h \leq 0 \end{cases}, \tag{4}$$

where $\eta \in \{0, 1\}$ is a constant expressing the ratio between h and the cosine amplitude, and $\vec{r}_v$ depends on the initial state. Figure 2 shows the result of a simulation of a discrete 2D network. Similarly to [8], when the network receives a constant excitatory global activation, it will converge to an *active state*, in which the amplitude of the population vector is amplified proportionality to the external activity. Conversely, when the external activity is inhibitory, the network population coding will be turned *off*, each neuron becoming constant. This mechanism is known as *gain modulation* [7].

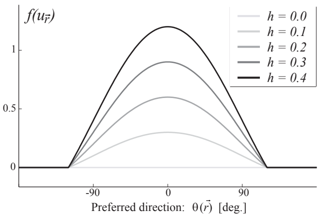

Figure 2: Response of a 2 dimensional discrete neural population u_r to a constant input h. $\eta = 0.5$, and $\mathrm{d}\theta = 1°$.

Let us now consider the case where the network receives a vectorial input $x_{\vec{r}} = \beta_{v_0}\,(\vec{r} \cdot \vec{r}_{v_0})$. Each unit converges, then, towards:

$$u_{\vec{r}} = \frac{1}{\chi}\,\beta_{v_0}\,(\vec{r} \cdot \vec{r}_{v_0}) = \frac{1}{\chi}(\vec{r} \cdot \vec{v}_0) \tag{5}$$

where χ is a constant (see table 1). In this case, the population activity simply reflects its inputs. Finally, by a linear approximation, we can get the general solution for both contributions of equation 3 that will be used in the next sections:

$$u_{\vec{r}} \approx \alpha\left(1 + \frac{1}{\eta}(\vec{r} \cdot \vec{r}_{v_0})\right) + \frac{1}{\chi}\,\beta_{v_0}\,(\vec{r} \cdot \vec{r}_{v_0}). \tag{6}$$

4 Vectorial Projection across FR

As illustrated on figure 3(a), the projection of a vector from a N-dimensional referential R to a N-dimensional referential R' can be decomposed into one translation from the origin O to the origin O' and N rotations, performed serially on $\{\phi_1, ..., \phi_N\}$.

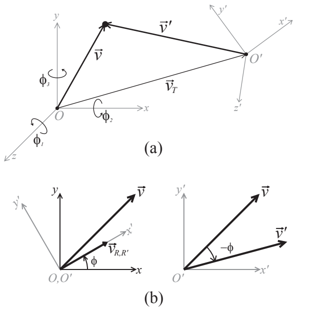

Figure 3: 3D FR transformations decomposed into three rotations and one translation at the origin (a). Rotation in a plane (b).

4.1 Translation

Let $\vec{v}$ be a vector in referential R represented by the population Ω_R, and $\vec{v}'$ its projection in the referential R' represented by $\Omega_{R'}$. Assuming that $\vec{v}_T$ is the vector across the origins of the referentials, the translation is performed by applying an input $x_{\vec{r}} \propto (\vec{r} \cdot \vec{v}) - (\vec{r} \cdot \vec{v}_T)$ to the population $\Omega_{R'}$. By 5, the population vector of $\Omega_{R'}$ will converge to $(\vec{v} - \vec{v}_T) = \vec{v}\,'$.

4.2 Rotation

Let ϕ be the angle of rotation between the two planar referentials R and R' (see fig. 3(b)), with superposed origins $O = O'$, and $\vec{v}_{R,R'}(\phi) \propto (\cos(\phi), \sin(\phi))$ the vector determining that angle, encoded in the population $\Omega_{R,R'}$. Let Ω_R and $\Omega_{R'}$ be two populations coding for the vector $\vec{v}$ and its projection $\vec{v}\,'$. In order to perform the rotation, we need to define an intermediary population, *the gain field* Ω_{GF}. Its architecture (see fig. 4) can be seen as a two dimensional planar population where the neurons, denoted by $u^{\mathrm{GF}}_{\vec{r},\vec{s}}$, are simultaneously sensitive to two preferred directions $\vec{r}$ and $\vec{s}$ related to the inputs incoming from Ω_R and $\Omega_{R,R'}$, respectively. The network's dynamic is governed by equation 2. Note that the lateral weights, responsible for the gain modulation, are distributed along one dimension only, namely

$$w^{\mathrm{GF}\to\mathrm{GF}}_{(\vec{r}',\vec{s}')\to(\vec{r},\vec{s})} = \begin{cases} \gamma\,(\vec{s}\cdot\vec{s}\,') & \vec{r} = \vec{r}\,' \\ 0 & \vec{r} \neq \vec{r}\,' \end{cases} . \qquad (7)$$

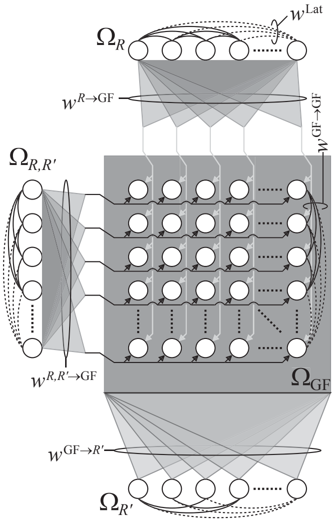

Figure 4: Network architecture.

The external inputs to the gain field are applied following

$$x^{\mathrm{GF}}_{\vec{r},\vec{s}} = \underbrace{\oint_{\Gamma_R} w^{R\to\mathrm{GF}}_{\vec{r}\,'\to\vec{r}}\; f(u^{R}_{\vec{r}\,'})\,\mathrm{d}\vec{r}\,'}_{(\vec{r}\cdot\vec{v})} + \underbrace{\oint_{\Gamma_{R,R'}} w^{R,R'\to\mathrm{GF}}_{\vec{r}\,'\to\vec{s}}\; f(u^{R,R'}_{\vec{r}\,'})\,\mathrm{d}\vec{r}\,'}_{(\vec{s}\cdot\vec{v}_{R,R'})} \qquad (8)$$

with $w^{R\to\mathrm{GF}}_{\vec{r}\,'\to\vec{r}} = \frac{2}{\pi}\chi(\vec{r}\cdot\vec{r}\,')$ and $w^{R,R'\to\mathrm{GF}}_{\vec{r}\,'\to\vec{s}} = \frac{2}{\pi}\chi(\vec{s}\cdot\vec{r}\,')$. Due to the lateral connectivity, the subset of neurons having the same preferred direction $\vec{r}$, have a convergence activity described by equation 6. If we replace the inputs, we obtain

$$u^{\mathrm{GF}}_{\vec{r},\vec{s}} \;\approx\; \frac{1}{\chi}\beta_{\vec{v}_{R,R'}}(\vec{s}\cdot\vec{r}_{\vec{v}_{R,R'}}) + \beta_{\vec{v}}(\vec{r}\cdot\vec{r}_{\vec{v}})\left(1 + \frac{1}{\eta}(\vec{s}\cdot\vec{r}_{\vec{v}_{R,R'}})\right). \qquad (9)$$

The synaptic weights from the gain field to the output population are

$$x^{R'}_{\vec{r}} = \oint_{\Gamma_{\mathrm{GF}}} w^{\mathrm{GF}\to R'}_{(\vec{r}',\vec{s}')\to\vec{r}}\; f(u^{\mathrm{GF}}_{\vec{r}',\vec{s}'})\,\mathrm{d}\vec{r}\,'\mathrm{d}\vec{s}\,' \qquad w^{\mathrm{GF}\to R'}_{(\vec{r}',\vec{s}')\to\vec{r}} = \frac{\eta\gamma}{\pi}\,(\vec{r}\cdot(\vec{r}\,'/\vec{s}\,')). \qquad (10)$$

In analogy to the complex division, we express the rotation of a unitary vector $\vec{r}$ by minus the angle given by the unitary vector $\vec{s}$ as $\vec{r}/\vec{s}$. As a result, we obtain, in the representation of the population $\Omega_{R'}$, a vector $\vec{v}\,'$ approximatively equal to $\vec{v}$ rotated by an angle $-\phi$

$$u^{R'}_{\vec{r}} \approx \beta_{\vec{v}}\big(\vec{r}\cdot(\vec{r}_{\vec{v}}/\vec{r}_{\vec{v}_{R,R'}})\big) = \big(\vec{r}\cdot(\vec{v}/\vec{r}_{\vec{v}_{R,R'}})\big). \qquad (11)$$

A simulation of our results is illustrated on figure 5. We show the activity of the four populations involved in the transformation. The shift in the direction representation depends on the discretization but is almost negligible, whereas the relative error on the amplitude given by $E(\|\vec{v}\|, \|\vec{v}\,'\|) = \frac{|\|\vec{v}\,'\| - \|\vec{v}\||}{\|\vec{v}\|}$ (see fig. 7), is the result of the approximations made in our development.

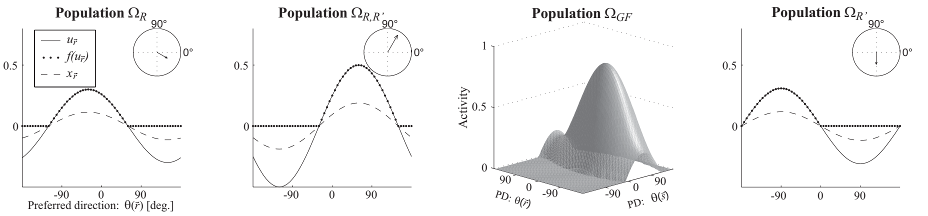

Figure 5: Attractor state of a discrete simulation involving 3600 for the population gain field and 60 neurons for all other populations. The inputs (dashed line), membrane potentials (dotted line) and activities (filled line) are plotted against the preferred direction of each neuron. The constants are set using $\eta = 0.5$. The corresponding population vector is shown at top right of each figure.

	$N = 2$	$N = 3$
γ	$(\eta\sqrt{1-\eta^2} + \mathrm{acos}(-\eta))^{-1}$	$\frac{3}{\pi}(2 + 3\eta - \eta^3)^{-1}$
χ	$(1 - \gamma\frac{\pi}{2})$	$(1 - \gamma\frac{2\pi}{3})$

Table 1: Expression of the constants defined in the text depending on the dimension of the population and on the value of parameter $\eta \in]0, 1[$. The use of either 2 or 3 dimensional constants in the synaptic weights depends on the dimension of the presynaptic population.

4.3 Extension to 3D rotation

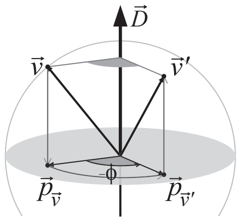

Figure 6: Rotation in 3D space reduced to planar rotation.

There is no major difference between a rotation around an axis in 3D and one in 2D, because the former can be reduced to the latter. Intuitively, as illustrated in figure 6, a rotation in 3D space can be seen successively as 1) a projection of $\vec{v}$ on the plane perpendicular to the rotation axis $\vec{D}$, 2) a rotation of an angle ϕ around $\vec{D}$ and 3) the restoration of the component parallel to $\vec{D}$ lost during the projection. Thus, the synaptic weights originating from Ω_R are set such that $w^{R\to\mathrm{GF}}_{\vec{r}'\to\vec{r}} = \frac{3}{2\pi}\chi\,(\vec{r}\cdot\vec{p}_{\vec{r}'})$, where $\vec{p}_{\vec{r}} = \vec{r} - (\vec{r}\cdot\vec{D})\,\vec{D}$[2] is the projection of the preferred direction $\vec{r}$ on the plane perpendicular to the axis $\vec{D}$. We can then replace the first term of equation 8 with $(\vec{r}\cdot\vec{p}_{\vec{v}})$. Finally, by slightly changing the weights $w^{\mathrm{GF}\to R'}$ and by adding new synaptic links from Ω_R to $\Omega_{R'}$[3], we are able to feed the output 3D population with the rotated projected vector and the vectorial component lost in the projection, namely

$$w^{\mathrm{GF}\to R'}_{(\vec{r}',\vec{s}')\to\vec{r}} = \frac{\eta\gamma}{\pi}\,(\vec{p}_{\vec{r}}\cdot(\vec{r}'/\vec{s}'))(\vec{r}\cdot\vec{p}_{\vec{r}}) \qquad w^{R\to R'}_{\vec{r}'\to\vec{r}} = \frac{3}{2\pi}\chi\,(\vec{r}'\cdot\vec{D})(\vec{r}\cdot\vec{D}). \quad (12)$$

As a result, the output population $\Omega_{R'}$ converges to a stable activity, equal to

$$u^{R'}_{\vec{r}} \approx \big(\vec{r}\cdot(\vec{p}_{\vec{v}}/\vec{r}_{\vec{v}_{R,R'}})\big) + (\vec{r}\cdot(\vec{v}\cdot\vec{D})\vec{D}) = (\vec{r}\cdot\vec{v}'). \quad (13)$$

where both terms correspond respectively to the rotated projection of vector $\vec{v}$, and its component parallel to $\vec{D}$.

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[2] with $\|\vec{D}\| = 1$

[3] not shown on figure 4

5 Discussion

We have shown how a neural mechanism based on population vector coding can perform vectorial operations, such as translations and rotations. This suggests that population coding could be the neural basis of transformations across frames of reference.

Note that the model's hypothesis that 3D FR transformations are performed serially is in line with the *gradient hypothesis* for sensorimotor transformations [2]. However, the model's assumption that a FR is represented by a population of neurons, having an uniform distribution of preferred direction and exhibiting a cosine tuning curve that depends on the coding direction, is not representative of all neurophysiological data[4].

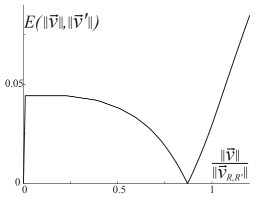

Figure 7: Error relative to the input amplitude. Same simulation parameters as in fig. 5 were used.

Acknowledgments

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