# Signature of an anticipatory response in area V1 as modeled by a probabilistic model and a spiking neural network

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Abstract-As it is confronted to inherent neural delays, how does the visual system create a coherent representation of a rapidly changing environment? In this paper, we investigate the role of motion-based prediction in estimating motion trajectories compensating for delayed information sampling. In particular, we investigate how anisotropic diffusion of information may explain the development of anticipatory response as recorded in a neural populations to an approaching stimulus. We validate this using an abstract probabilistic framework and a spiking neural network (SNN) model. Inspired by a mechanism proposed by Nijhawan [1], we first use a Bayesian particle filter framework and introduce a diagonal motion-based prediction model which extrapolates the estimated response to a delayed stimulus in the direction of the trajectory. In the SNN implementation, we have used this pattern of anisotropic, recurrent connections between excitatory cells as mechanism for motion-extrapolation. Consistent with recent experimental data collected in extracellular recordings of macaque primary visual cortex [2], we have simulated different trajectory lengths and have explored how anticipatory responses may be dependent on the information accumulated along the trajectory. We show that both our probabilistic framework and the SNN model can replicate the experimental data qualitatively. Most importantly, we highlight requirements for the development of a trajectory-dependent anticipatory response, and in particular the anisotropic nature of the connectivity pattern which leads to the motion extrapolation mechanism.

#### I. INTRODUCTION

# A. Neural signature: motion anticipation, neural delays and pre-development of responses to predictable trajectories

A smooth visual motion generates a continuous stimulation of the classical receptive fields (CRFs) corresponding to the retinotopic representations of the trajectory in the primary visual cortex. Classically, it is believed there exists a facilitation of the neural activity following this trajectory of motion. This facilitation is thought to be favoring smooth, predictable trajectories compared to a flashed stimulus, unpredictable one, see [3] for a review. This difference is a potential mechanism for the flash-lag effect (FLE): Indeed, the FLE is a well investigated illusion that highlights the differences

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Fig. 1. Problem statement: correct localization of a ball despite neural delays. This picture illustrates the restrictive effect of delays at sensory and motor levels. We define a simplified but realistic setting where the time needed for the retinal image to reach the visual areas implicated in motion detection is equal to  $\tau_s$ . A further axonal time  $\tau_m$  is required to reach the oculomotor muscles. Note that the red dotted line indicates the position of the ball when its image formed in the retina reaches the visual system, while the gaze of the player is directed to its actual position in an anticipatory fashion (red solid line). In addition, the player should make a suitable motor command (direction of racket, black dashed line) to match the expected position of the ball at the future point in time of the hit (red dashed line).

associated with position coding of stationary flashed and moving stimuli [4], [5]. There is a lively debate surrounding the question which neural mechanisms correlate with the FLE.

Furthermore, these perceptual phenomena seem closely linked with the mechanisms compensating for axonal and processing delays in the visual system. A prototypical example is the problem faced by a tennis player (see Fig 1): the time needed for the neural signal to transfer motion information of the ball to the responsible areas in the cortex is around 50 ms [4]. If the ball is moving at 20 m  $\cdot$  s<sup>-1</sup>, it will travel approximately one meter. Considering this, one could first imagine that motion information arriving in cortex may represent the position of the ball as it comes in, that is corresponding to about 50 ms back in the past. Nevertheless, the near-prefect performance of the tennis player in locating the target —as can be suggested by the direction of his gaze- suggests the existence of a more precise representation of sensory information corresponding to the actual, present position of the ball. Both the FLE and this simplified example of a tennis player highlight that information accumulated from the motion trajectory may contribute in the development of an anticipatory response

in the neural populations which have their CRF stimulated by an approaching stimulus.

Herein, we focus on primates' primary visual cortex. Indeed, about a quarter of cells in this area are significantly sensitive to motion (speed or direction) [6]. To validate the hypothesis of Nijhawan [3], we study their potential role of the representation of the position of a moving dot in a system confronted with an inherent axonal delay. In that direction, experimental data recorded in V1 of macaque monkey [2] supports the hypothesis that neural populations develop an anticipatory response depending on the trajectory length before the arrival of the stimulus at the recorded CRF (see Fig 2). We will therefore use this neural signature throughout this study and compare this experimental data qualitatively with models of motion-based prediction. These models were introduced in our previous studies, at an abstract, Bayesian scale [8] and as spiking neural network (SNN) [9].

### B. Experimental protocol of neuronal signature

The neural signature associated with this study is extracted from extra-cellular recordings of neurones from area V1 in the macaque monkey [2], while a smoothly moving stimulus is approaching the CRF that was mapped for each neuron. The stimulation protocol includes three stimuli with different trajectory lengths between the start point of motion and the CRF. The recordings show a dynamic build up of an anticipatory response before the arrival of the stimulus at the CRF. This anticipatory response is systematically dependent on the length of trajectory (see Fig 2).

To investigate the trajectory dependent anticipatory response, we have conducted equivalent experiments in our modeling framework. In the electrophysiological protocol the recorded population is fixed and there are three different trajectory lengths. In our model experiments, we have studied the estimated position of the stimulus at three successive points along the same the trajectory. Thus, both electrophysiological protocol and simulated model aim at studying the importance of the trajectory length in the temporal profile of neural responses.

# *C.* Hypothesis: Temporal coherence of motion and internal representation of predictable trajectories

Prior information on regularities of the world is essential for optimal performance of sensory processing. In the particular case of detecting visual motion, the prior knowledge on the temporal coherence of motion may facilitate the estimation of predictable trajectories and contribute to the compensation of neural transfer delays.

### D. Model: motion-based prediction

Based on such prior information, we propose a generic Bayesian modeling framework to implement anisotropic diffusion of the estimated motion information. This framework may serve as an internal predictive representation of motion trajectories to overcome neural delays. In the model, we aim to asses the role of prediction in the dynamical development of such a neural activity at, or before, the arrival of the



Fig. 2. (**Top**) Experiment: a smoothly moving stimulus (tilted bar) is approaching the classical receptive field (CRF) mapped from a V1 neuron. The activity is recorded for different length of the trajectory before it enters the CRF. (**Bottom**) Extracellular spiking response (in spikes per second) averaged over a population of macaque monkey V1 neurons. This shows an anticipation of the response with respect to the trajectory length (adapted from Benvenuti et al [2])

sensory stimulus. To explore if such diffusive predictive mechanisms could explain neurophysiological recordings we simulated similar experiments in our model by using two different configurations of the model: **MBP** (Motion-based **prediction**), in which model holds an internal representation of the motion trajectory by predicting the position and velocity of the stimulus and **PBP** (position-based prediction) in which the model holds an internal representation of trajectory by predicting *only* its position.

#### E. Motion-based prediction with spiking neurons

In our previous study [9], we have shown that motionbased prediction can be implemented in a SNN through anisotropic connectivity. Anisotropic connectivity can be seen as an essential mechanism to diffuse information neural networks so that local motion-information is integrated to a coherent percept, allowing the prediction of the trajectory of a moving stimulus. Here, we use this model to study the role of connection delays and focus on the anticipatory response reflected in the spike activity of the network.

We have chosen to use a SNN and not used a rate-based or mean-field description for the neural network for several reasons. First, SNN models are biologically more plausible as they can capture temporal behavior close to their biologically counterpart. Second, our study aims to provide computational models for neuromorphic platforms designed for SNN [11], [12]. Third, SNN have the advantage that network communication is required only when spikes occur in contrast to rate-based model which require continuous communication between nodes and hence have scaling limitations.



Fig. 3. (Left) Diagonal model of motion-based prediction: considering  $\tau$  as neural delay, there is no measurement at t = 0 and ultimate state estimation at any time step is z(t). Diagonal scheme of motion estimation includes two steps: first, the motion state  $z_{t-\tau}$  is estimated based on smoothness constraint and delayed sensory information  $I_{t-\tau}$ , then according to a prior knowledge on late arrival of sensory information, the response is extrapolated for a period of a "virtual blank" of duration  $\tau$ , without any sensory measurement. (**Right**) Neural implementation of the diagonal model. We represent the connection from neuron *i* (bottom layer) to neuron *j* (upper layer) knowing its latency  $\tau_{ij}$  and the preferred position of neuron *j* (horizontal axis  $x_j$ ) and speed (vertical axis  $v_j$ ). To implement motion-based prediction, each neuron favors input which is coherent with a smooth trajectory, collecting information from neurons with a similar preferred speed around  $v_i = v_i$  but at a position which is predicted to be around  $x_i = x_j - v_i \cdot \tau_{ij}$ .

# II. MODEL: MOTION-BASED PREDICTION WITH AXONAL DELAYS

As mentioned before, this paper aims to study the role of predictability of trajectory on development of early response in neural populations, possibly distant from cortical position of stimulus. Predictability of stimulus is modeled in a Bayesian framework by a probabilistic representation of motion. The motion of an object in the planar visual space at a given time is fully described by the probability distribution of its position and velocity. In such a framework, Bayesian inference optimally integrates sensory information coming from the scene (the likelihood) with what is suggested by the internal model, the priors defining for instance the smoothness of the trajectory. Finally, Bayes rule allows to infer the posterior estimation. To study the effect of delays, our Bayesian framework integrates sensory information from the recent past by integrating the knowledge of this fixed delay within the internal model.

#### A. Diagonal model and delayed access to sensory input

Considering neural delays, predictive position coding can be implemented by pushing the population response forward in the direction of motion. Our model uses the motion signal including position and velocity of a moving object to extrapolate the trajectory which is most likely to be covered by the stimulus. As illustrated in Fig 3, a classical Markov chain for state estimation of the stimulus can be redrawn in a diagonal fashion.

This diagonal scheme of motion states illustrates the dependence of the extrapolated state  $z_t = \{x_t, y_t, u_t, v_t\}$  to the state suggested by the delayed motion information  $z_{t-\tau}$ , where  $\tau$  is the value of the delay in terms of frame number (in our simulations each frame has been arbitrarily mapped to 10 ms of biological time). In this way, the earliest part of any trajectory would be missed, because motion estimation starts at  $t = \delta_t - \tau > 0$  and there is no sensory information at

t = 0. The next states are realistic estimations of the actual position of the stimulus and trajectory prediction overcomes the restrictive effect of delay. The diagonal model of motion extrapolation was originally proposed by Nijhawan [1] to explain the detailed mechanism of motion extrapolation by retinal ganglion cells. Here, we use this idea as an abstract rule for predictive motion estimation. Considering delayed access to sensory input in diagonal model (see Fig 3), master equations of model can be written as below: Considering the delayed access to sensory input in diagonal model (see Fig 3), master equations of the model can be written as below:

Estimation:

$$p(z_{t-\tau}|I_{0:t-\tau}) \propto p(I_{t-\tau}|z_{t-\tau}) \cdot p(z_{t-\tau}|I_{0:t-\tau-\delta t})$$
(1)

Prediction:

$$p(z_{t-\tau}|I_{0:t-\tau-\delta t}) = (2)$$

$$\int dz_{t-\delta t} \cdot p(z_{t-\tau}|z_{t-\tau-\delta t}) \cdot p(z_{t-\tau-\delta t}|I_{0:t-\tau-\delta t})$$

Extrapolation:

$$p(z_t|I_{0:t-\tau}) \propto p(z_t|z_{t-\tau}) \cdot p(z_{t-\tau}|I_{0:t-\tau})$$
(3)

In the diagonal model, the motion state  $z_{t-\tau}$  is estimated based on delayed sensory input  $I_{t-\tau}$  and the smoothness of motion.  $\delta_t$  is the step size of estimation and  $\tau$  represents the imposed delay. Equation 1 calculates the probability of a desired motion state, using the likelihood of that state (measured by delayed sensory information), and the predicted state given by Eq 2. In the next step, estimated motion is extrapolated for a period of "virtual blank" of duration  $\tau$ during which there is no sensory measurement. Thus, the extrapolative step shown by equation 3 is purely predictive, using the smoothness constraint and prior information of the value of delay  $\tau$ .



Fig. 4. Anticipation mechanism: the anticipated position of the stimulus (a small dot moving horizontally with constant velocity) is illustrated for  $\tau = 100$  ms. The stimulus is moving from -1 to 0 (shown by dashed black lines, the white line representing the delayed position) and position estimations are illustrated as histograms composed of 400 positional bins. Color from blue to red represent the probability (from low to high) in each time bin. Sensory drive begins after a delay  $\tau = 100$  ms and the integration of motion estimates builds up gradually. Note that before that time, information is distributed uniformly over all positions. (Left) In the PBP model, a positional error occurs and the estimated position lags behind the actual position of the stimulus (probability distribution is centered around the dashed white line). (Right) In the MBP model, an anticipatory response develops gradually and the actual position of stimulus is accurately represented and approaches the dashed black line.

#### B. Motion-based prediction

The internal predictive representation favors smooth trajectories in two steps: First, temporal coherency of motion at each step (represented by  $p(z_{t-\tau}|z_{t-\tau-\delta t})$  in equation 2) is implemented by following equations:

$$x_{t-\tau} = x_{(t-\tau-\delta t)} + u_{(t-\tau-\delta t)} \cdot (\delta t) + \nu_x$$

$$u_t = u_{(t-\tau-\delta t)} + v_{(t-\tau-\delta t)} \cdot (\delta t) + \nu_x \tag{4}$$

$$g_{t-\tau} - g_{(t-\tau-\delta t)} + v_{(t-\tau-\delta t)} \cdot (\delta t) + \nu_y \tag{4}$$

$$u_{t-\tau} = \gamma \cdot y_{(t-\tau-\delta t)} + \nu_y$$

$$v_{t-\tau} = \gamma \cdot v_{(t-\tau-\delta t)} + \nu_v \tag{5}$$

$$\nu_x, \nu_y \propto \mathcal{N}(x, y; 0, D_X \cdot \delta t)$$
(6)

$$\nu_u, \nu_v \propto \mathcal{N}(u, v; 0, (\sigma_p^{-2} + D_V^{-1})^{-1} \cdot \delta t)$$
(7)

The noise terms  $\nu_x, \nu_y$  are drawn from Gaussian distributions: Position is blurred with diffusion parameter  $D_X \cdot \delta t$  and sampled at each time step. Blurring of velocity is done similarly with  $\nu_u$  and  $\nu_v$  by sampling from Gaussian distributions with variance  $(\sigma_p^{-2} + D_V^{-1})^{-1} \cdot \delta t$ . Here,  $\gamma = (1 + \frac{D_V^2}{\sigma_a^2})^{-1}$ is the damping factor introduced by the prior information on slowness of motion and  $\gamma \approx 1$  for a high value of  $\sigma_p$ . As defined in [14], prior information in slowness and smoothness of motion can be parameterized by the variance  $(\sigma_p^{-2} + D_V^{-1})^{-1} \cdot \tau$  on velocity. The noise terms  $\nu_x, \nu_y$ are drawn from Gaussian distributions: Position is blurred with diffusion parameter  $D_X \cdot \delta t$  and sampled at each time step. Blurring of velocity is done similarly with  $\nu_u$  and  $\nu_v$  by sampling from Gaussian distributions with variance  $(\sigma_p^{-2} + D_V^{-1})^{-1} \cdot \delta t$ . Here,  $\gamma = (1 + \frac{D_V^2}{\sigma_p^2})^{-1}$  is the damping factor introduced by the prior and  $\gamma \approx^{p} 1$  for a high value of  $\sigma_p$ . As defined in [14], prior information in slowness and smoothness of motion can be parameterized by the variance  $(\sigma_p^{-2} + D_V^{-1})^{-1} \cdot \tau$  on velocity. The update rule (see [10]

for a derivation) assumes independence of the prior on slow speeds with respect to predictive prior on smooth trajectories.

Second, estimated motion is extrapolated forward, for the duration of  $\tau$  and based on the knowledge from trajectory and a prior knowledge on the fixed delay  $\tau$ . As we assume the noise to be independent, this step can be computed with  $p(z_t|z_{t-\tau})$  in equation 3 and simply defined by equations similar to equations 4-5:

$$x_t = x_{t-\tau} + u_{t-\tau} \cdot (\tau) + \omega_x$$
  

$$y_t = y_{t-\tau} + v_{t-\tau} \cdot (\tau) + \omega_y$$
(8)

$$= \gamma \cdot u_{t-\tau} + \nu_u \tag{0}$$

$$v_t = \gamma \cdot v_{t-\tau} + \nu_v \tag{9}$$

$$\omega_x, \omega_y \propto \mathcal{N}(x, y; 0, D_X \cdot \tau) \tag{10}$$

$$\omega_u, \omega_v \propto \mathcal{N}(u, v; 0, (\sigma_n^{-2} + D_V^{-1})^{-1} \cdot \tau)$$
(11)

This Bayesian motion estimation has been implemented in a particle filtering framework.

In particular, the mapping between input and predictive layers is anisotropic. For instance, in the case of rightward motion, the predictive layer may be interpreted as a neural population which gets stimulated by sensory information received by neurons left of the target. Note that the diagonal representation does not change fundamentally the motionbased prediction model that we presented in [8]. By introducing a prior knowledge on delays  $\tau$  this representation provides distinct layers for demonstrating the delayed arrival of stimulus related information and predictive neural activities. As a consequence, motion-based prediction explains the anticipatory response of V1 neurons solely using the hypothesis of predictive internal representation of motion. As a control model we have used the PBP configuration which does not predict the velocity of stimulus. The comparison between two configurations reveals that having no prediction



Fig. 5. Anticipatory response in the diagonal model with  $\tau = 100$  ms, while a smoothly moving stimulus is approaching to three target points in the trajectory. The relative position of points in the trajectory is shown in the inset box and estimated position of stimulus by MBP and PBP models at those locations is illustrated by the corresponding color. Responses are averaged over 10 trials and centered at the time of the stimulus arrival at the target position (white dotted line). The white dashed line indicates the time at which the delayed stimulus information reaches each target position

for the stimulus velocity leads to a delayed and less localized response.

# C. Results

Results of the abstract motion estimation framework are illustrated in Fig 4 and Fig 5. The stimulus is a horizontally moving dot with constant speed. The estimated position has been studied in the early part of the trajectory and results are averaged over 10 trials.

Fig 4 includes histograms of the estimated stimulus position by the diagonal MBP and the PBP model ( $\tau = 100 \text{ ms}$ ). In both models, motion estimation starts at  $time = \tau$ , as soon as the delayed motion information are detected by model. The actual and delayed positions of stimulus are indicated by black and white dashed lines, respectively. The probability of position estimates is color coded ranging from zero to one and is matched to the color range from dark blue to red. In MBP model, despite the delayed arrival of motion information, position estimation is accurate and match the actual position of stimulus. The PBP model provides a delayed and poor motion estimation, as reflected by the difference between the dashed line and the center of estimated position. By advancing in the trajectory, the MBP model corrects the positional error caused by the delay (note the shift of peaks toward zero in Fig 5), while the estimated position by PBP model remains lagged. The dynamics of estimated position by both models is illustrated in Fig 5. In order to simulate the experimental protocol in V1 [2], three successive points in the trajectory have been selected. The temporal profile of the estimated positions are shown in a centered fashion, i.e. the profiles are shifted by the stimulus arrival time.

In addition, the diagonal MBP model reproduces the dependence of position coding on the trajectory length. In other words, the positions located ahead of the current stimulus position develop an anticipatory response before the arrival of the stimulus. The temporal profile of the estimated position by diagonal PBP model is not dependent to the relative position of stimulus in the trajectory.

#### III. SPIKING NEURAL NETWORK (SNN)

The SNN used in this study is based on our previous study [9] and aims at incorporating the mechanism for delay compensation. The network in [9] consisted of one population of excitatory neurons and one population of inhibitory neurons with recurrent connections within each population and between the two populations. Each neuron was implemented as a leaky integrate-and-fire neuron with conductance-based exponential synapses (for a full description, see [9]). Simulations were performed with PyNN [15] as interface to the NEST simulator [16].

In contrast to the Bayesian framework described above, we have implemented our SNN model in one dimension for simplicity. Using a two dimensional description is equally possible in the SNN (as shown in our previous study [9]), but requires larger networks in order to get a sufficient coverage of the tuning space and is computationally more costly to simulate. In order to show that connectivity is sufficient to implement delay compensation and that a trajectorydependent motion-anticipation signal emerges in the SNN model, a one dimensional description is sufficient.

### A. Tuning properties

In order to transform the visual input into neural activity we define tuning properties as follows. Each cell in the excitatory population has two tuning properties, one preferred velocity  $v_x$  and the position of the CRF x, i.e. the stimulus position preferred by the cell. Preferred velocities are distributed according to a distribution favoring low velocities [14], with a logarithmic scale for the speed according to Weber's law [13]. CRF centers are randomly distributed in the interval (0, 1). For a stimulus at position  $x_{stim}$  moving with speed  $v_{stim}$  we calculate the input spike rate for an inhomogeneous Poisson process inserted into cell i as:

$$L_{i}(t) = f_{max} \cdot \exp(-\frac{\|x_{stim}(t) - x_{i}\|^{2}}{2\beta_{X}^{2}} - \frac{\|v_{stim} - v_{i}\|^{2}}{2\beta_{V}^{2}})$$
(12)

where  $\beta_X = 0.05$  and  $\beta_V = 0.05$  describe how diffuse the stimulus appears and  $f_{max}$  is the maximum input frequency of 1000 Hz.

Each cell receives the input stimulus delayed by 100 ms.As in the diagonal MBP model described above (see Fig 3), we correct for this delay by predicting the past position of the input specifically to each cell *i*:

$$x_{i,stim}(t) = x_{0,stim} + v_{stim} \cdot t - v_i \cdot \tau \tag{13}$$

where we set  $\tau = 100$ ms in the MBP model to compensate for the perceptual delays. Inhibitory cells do not have tuning properties, but the model could be extended to allow for anisotropic connectivity involving the inhibitory cells.

#### B. Network connectivity

Similar to our previous study, we use the excitatory cell's tuning properties to calculate the recurrent connections strengths within the excitatory population. Connections from the excitatory to the inhibitory population (and vice versa) and the recurrent inhibitory connections are set up according to a distance dependent isotropic scheme with 2% probability as described in [9]. For each excitatory source cell *i* we calculate the connection strength  $p_{ij}$  to each possible target neuron *j* according to Equation 14. Each excitatory neuron connects to the 0.5% of all possible excitatory targets with the highest strength, other connections are discarded.

$$p_{ij} = \exp(-\frac{\|\vec{x}_i^* - \vec{x}_j\|^2}{2 \cdot \sigma_X^2}) \cdot \exp(-\frac{\|\vec{v}_i - \vec{v}_j\|^2}{2 \cdot \sigma_V^2})$$
(14)

$$\vec{x}_i^* = \vec{x}_i - \vec{v}_i \cdot \tau_{ij} \tag{15}$$

Where  $\vec{x}_i^*$  is the position where the source neuron *i* predicts the stimulus to be after a certain time  $\tau_{ij}$ , see Fig 3.

This connection rule is valid both for the recurrent connections and the mapping from the input to the excitatory population. For lateral interactions, assuming a constant propagation speed in the lateral interactions within the excitatory population, delay is proportional to the cortical distance. In particular, we will use here for the MBP implementation a fixed axonal delay from the sensory layer  $\tau = 100 \text{ ms}$  (and corresponding to the physical axonal delay). For biological plausibility but also to allow future implementation on neuromorphic chips, we used a fixed latency between neurons in the excitatory layer  $\tau_{ij} = 5 \text{ ms}$  and a cortical distance proportional to the retinotopic one.

By pushing the motion information gathered at position  $x_i$  forward by  $\vec{v}_i \cdot \tau_{ij}$  the connectivity becomes anisotropic and the network is able to compensate for the neural and perception delays. The parameters  $\sigma_X$  and  $\sigma_V$  in Eq 14 determine the effect of the tuning properties on the resulting connectivity as in Eqs 5 and 11. In particular, the MBP model corresponds to  $\sigma_V = 0.1$  and  $\sigma_X = 0.1$ . The abstract PBP model corresponds to  $\sigma_V \to \infty$ , that is, where information on speed is uniformly represented. As a consequence in the PBP model, anisotropy only acts in the spatial dimension and the prediction from Eq 14 becomes isotropic. The left part in Figure 6 shows the outward connection strengths for one example source cell for both setups.

#### **IV. SIMULATION RESULTS**

We have simulated networks with 20000 excitatory neurons and 5000 inhibitory neurons using two different connectivity patterns across the excitatory population with  $\sigma_V = 0.1$  and  $\sigma_V = 100$  corresponding to the PBP and MBP models in the abstract framework, respectively. The network is stimulated with a blurry dot moving at a constant speed starting at position 0.1 and moving rightward with a speed of 0.5 s<sup>-1</sup>.

In order to read out the motion information processed in the SNN we have used the vector-averaging approach described in [9]. In short, we have binned the output spike trains in time bins of 25 ms and sorted them according to the emitting cell's tuning preference. Finally, we normalized the output rate across the population to obtain a measure for the confidence of the network prediction. Figure 7 shows the readout of the network prediction for the two different connectivities. The two color maps show the network's confidence about the motion information color coded for the two different connectivity configurations.



Fig. 7. Prediction confidence in the SNN with **MBP** (**Upper**) and **PBP** (**Bottom**) connectivity. Cells are sorted according to their CRF centers and spike rates are time-binned and normalized over the number of cells to derive the prediction confidence. The black dashed line indicates the actual position of the stimulus and is ahead of the networks activation 'wave'. The white dashed line shows the delayed position of the stimulus. In the network with **MBP** connectivity the network follows the actual position more closely compared to the network with **PBP** connectivity.

As Figure 7 shows, the PBP network is not able to compensate for delays and information about the stimulus speed is not diffused within the network due to the isotropic connectivity, the readout lags behind the actual stimulus movement. In contrast, the readout in MBP network follows the real stimulus more closely.

A comparison of the two connectivity configurations, regarding the activity and the derived confidence about the stimulus position, shows that our SNN implementation gives qualitatively equivalent results as shown in the abstract framework and seen in physiological experiments. The network with PBP connectivity does not compensate for perceptual delays and loses information about the stimulus speed as the connectivity is insensitive to the cells' preferred



Fig. 6. Connectivity profile in the SNN. Both figures show the outward connection probability for one example cell as color code. Excitatory cells are displayed as black dots in the tuning space, the x-axis shows the center of the cells' receptive fields, the y-axis shows the preferred speed. Realized connections from the source cell (indicated by the yellow star) are shown as white circles with the relative connection strengths indicated by the radii of the circles. The green diamond indicates the center of mass for all outward connections from the source cell. Left: PBP connectivity ( $\sigma_X = 0.1, \sigma_V = 100.$ ). As the connectivity is insensitive to preferred speeds, the connectivity is isotropic in the speed dimension. The bias of the network for slow speeds can be seen in the denser distribution of cells around small preferred speeds. **Right**: The MBP connectivity pattern connects cells according to their preferred speed and position ( $\sigma_V = 0.1, \sigma_X = 0.1$ ). As the source cell codes for rightward motion the preferred projection site is shifted in the direction of the motion for which the source codes. The center of mass for outgoing connections is only slightly shifted rightwards as connections are restricted to delays in a biologically plausible range.

directions. The PBP network still shows some anticipatory response, but as shown in Fig 7 and Fig 8 the confidence peak occurs after the stimulus has passed the cells' CRF and lags behind the MBP prediction due to the diffusion of outdated motion information. In contrast, the MBP model integrates all relevant motion information along the trajectory and diffuses it within the network which is necessary to build up a trajectory dependent anticipatory response.

## V. CONCLUSIONS

In this paper, we have studied position coding of a stimulus moving in a coherent trajectory, with the hypothesis of motion-based predictive coding and by taking neural delays into account. We have modeled the anticipatory signature of position coding in an abstract Bayesian model and a SNN model and our results are consistent with experimental evidence on trajectory dependent motion integration reported in [2] and [7].

In the abstract model, implemented in a Bayesian framework with a prior on coherency of trajectory, our main hypothesis is based on the anisotropic diffusion of motion information gained from trajectory of stimulus. Particularly, in this work we have focused on the restrictive effect of neural transfer delays and have proposed a diagonal motion estimation framework which extrapolates the estimated position in the direction of the trajectory to compensate for the delayed arrival of sensory information. The diagonal motion extrapolation model proposed in this study, is a generalization of a model proposed by Nijhawan [1] to explain the motion extrapolation mechanism believed to occur in the retina. Here, we suggest that there may be a general delay compensatory mechanism which can partly take place at any motion processing area of the visual hierarchy.

We have implemented our model experiments in a similar

fashion as the experimental protocol of a electrophysiological study in macaque monkey [2]. In the abstract framework we have implemented two configurations of model: motionbased prediction (MBP) and position-based prediction (PBP). In both configurations, the model receives sensory input which codes the state of visual scene at some frames back in time and the estimated motion is based on delayed stimulus information.

Our results show that the MBP model can effectively extrapolate the motion trajectory and lead to a correct estimation of the actual stimulus position, while the position estimated by the PBP model corresponds to the delayed sensory information with no delay compensation. In addition, unlike the PBP model, the MBP model can also reproduce the trajectory dependent nature of the anticipatory response. This means that having integrated over a longer trajectory would lead to a temporally more distributed estimated response.

Our implementation of the SNN shows qualitatively the same results. Differences between the MBP and PBP configurations of SNN model are entirely based on the different connectivity patterns. The MBP implementation with anisotropic connections for the input and recurrent connections makes use of all relevant motion information (position and velocity) and is able to build up an anticipatory response along the trajectory. In contrast, the PBP model is isotropic in the speed dimension of the tuning space and thereby can not take advantage of this important motion information, which leads to the delayed and trajectory independent response.

In addition the MBP model compensates for accumulated delays by pushing the predicted position by sources cells further in the direction coded by the cell, leading to an anisotropic connectivity. In both modeling frameworks, PBP configuration serves a control simulation, to highlight the importance of velocity related sensory information in precise



Fig. 8. Confidence traces derived from the spiking activity. The y-axis shows the mean confidence averaged over a population 30 cells located at different positions, the x-axis represent time in ms. Population responses are aligned to the time when the stimulus arrives at the average position of the recorded population. Spike activity was filtered with an exponential function with 25 ms time constant and normalized across the network. The gray dotted line (left) indicates stimulus arrival at the mean position of the populations CRF. The gray dashed line (right) shows the delayed stimulus arrival. The black traces correspond to a population with CRF centered early in the trajectory, the red later and blue trace even later, respectively. Upper: The confidence traces of the MBP network show a trajectory dependent anticipatory signature, as the blue trace has its maximum at the time of stimulus arrival, whereas the black trace peaks a bit later. Due to the delay compensation mechanism, the response later in the trajectory matches the actual stimulus position better and resembles the experimental signature qualitatively (see Figure 2). Lower:) The network with the PBP does not show a robust trajectory dependence response as all three traces are similar. The responses lag behind the actual stimulus due to the lack of delay compensation.

position coding. As we have shown before in [9], anisotropic connectivity is crucial to implement motion-based prediction. Here, we have shown that anisotropic connectivity can also be used as a delay compensation mechanism.

There are extensive neural network studies dealing with motion detection tasks based on various learning and decoding algorithms. A model proposed by Rao et al [17] implements Bayesian inference of a hidden Markov model by interpretation of recurrent feedforward weights as log posteriors. In the current study we did not aim to build a network with Bayesian architecture, instead we have highlighted that motion-based anisotropic connectivity pattern in a SNN can produce results similar to an abstract Bayesian motion estimation model, being consistent with evidences of trajectory dependent motion integration in the visual cortex. Furthermore, we have emphasized the diagonal delay compensation mechanisms in our Bayesian model and suggested that it can be achieved by anisotropic connectivity.

Our results suggest that in cortical areas with retinotopic

organization (like V1 and MT), motion prediction may be set up via the anisotropic network connections. As a theoretical insight, setting the network with stronger anisotropy, would lead to capability of overcoming longer delays. While stressing the sufficiency of static anisotropic connectivity patterns to reproduce neural signatures of prediction, future work needs to integrate learning in the formation of connectivity for predictive coding through Bayesian learning rules [18]. Another perspective for extending our models can be addressing questions about predictive coding of smoothly curved trajectories. In theory, one can include an acceleration term for the speed and direction, in the internal model of Bayesian framework. Equivalently, acceleration selectivity can be added to the tuning properties of neurones in SNN model, even though there is no clear experimental evidences for existence of acceleration sensitive type of cells in the visual cortex. This would increase the complexity and computational cost of the model.

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