Active maintenance of binocular correspondence leads to orientation alignment of visual receptive fields

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Abstract—Neural development in the visual cortex depends on the visual experience during the so-called critical period. Recent experiments have shown that under normal conditions rodents develop binocular receptive fields which have similar orientation preferences for the left and right eyes. In contrast, under conditions of monocular deprivation during the critical period, this orientation alignment does not happen. Here we propose a computational model to explain the process of orientation alignment, its underlying mechanisms, and its failure in case of monocular deprivation or uncorrelated binocular inputs. Our model is based on the recently proposed Active Efficient Coding framework that jointly develops eye movement control and sensory representations. Our model suggests that the active maintenance of a binocular visual field, which leads to correlated visual inputs from the two eyes, is essential for the process of orientation alignment. This behavior is analogous to vergence control in primates. However, due to the fact that rodents have large receptive fields with low spatial frequency tuning, the coordination of the eyes need not be very precise. The model also suggests that it is not necessary that coordinated binocular vision be maintained continuously in order for orientation alignment to develop.

Index Terms—binocular vision, disparity tuning, orientation alignment, vergence control.

I. INTRODUCTION

The eye placement and movements of mammals vary \cite{1}. Primates have frontally placed eyes with a large amount of binocular overlap. This enables them to estimate depth based upon the disparities between the two views of the same environment provided by the two eyes. An important part of depth perception is the continuous control of the eyes to align the foveas of the two eyes so that their images are matched. Misalignments of more than one degree disrupt fusion. On the other hand, mammals such as rabbits have laterally directed eyes. While this provides for more coverage of the environment, there is only a small amount of binocular overlap (~10 degrees). The eye movements of these animals do not seem to be geared towards maintaining precise binocular alignment.

The eye placement of rodents, such as mice and rats, lies between lateral and frontal. This provides for a considerable (~40 degree) binocular field. However, it is not clear whether mice and rats exploit the same stereovision mechanisms as primates. Fully understanding the role of stereovision in rodent perception will require the synthesis of the results of neural and behavioral experiments via computational modelling. At the behavioral level, the model should account for the role of eye movements in perception. At the neural level, the model should account for the processing by the visual neurons obtaining input from the binocular region. These two levels are coupled because the rodent is embodied in the environment. The behavior of the rodent affects the statistics of the visual input. According to the efficient coding hypothesis \cite{2}, the statistics of the visual input affect the neural representation of that input, which in turn drives the behavior. Thus, the behavior and the neural representation which drives it should co-develop.

A key question that can be addressed by such a model is the possible role of an eye movement control strategy that maintains binocular alignment. The evidence that rodents use such a strategy is mixed. Behavioral experiments by Wallace et al. suggest that precise binocular alignment is not maintained in rats, although it appears that they do seek to maintain a large area of binocular overlap \cite{3-6}. On the other hand, a complete lack of alignment is inconsistent with neurophysiological evidence that mice possess disparity selective neurons with properties similar to those observed in primates \cite{7}. It is also at odds with the finding that the orientation of left and right monocular spatial receptive fields of binocular neurons in mouse primary visual cortex become more aligned during the critical development period, and that this orientation alignment is mediated by visual input \cite{8,9}. Both results suggest that the visual input from the left and right eyes to binocular neurons are correlated for a significant fraction of the time. This would only occur if the two eyes...
move in a coordinated fashion so as to establish and to maintain significant overlap of the monocular visual fields on the same surface in the environment, even in the presence of relative motion between the observer and the environment.

In this paper, we describe the first attempt to build a computational model that can account for these apparently disparate results. This model is based upon the Active Efficient Coding framework [10, 11], which has been used to account for the joint development of binocular neurons exhibiting orientation and disparity selectivity and vergence eye movement behavior to maintain binocular alignment. However, in contrast to previous work, here we consider the case where this alignment is not continuously maintained. Our main findings are that correlated visual input is required in order for disparity tuned neurons with orientation aligned monocular receptive fields to develop. This provides strong support for the maintenance of binocular alignment. The model is also consistent with the results of Wallace et al., as we show that this development does not require continuous maintenance of binocular alignment.

II. MODEL DESCRIPTION

The Active Efficient Coding framework used in this work consists of two main elements: a representation mechanism which encodes the binocular visual input and a control mechanism that alters the relative positioning of the eyes to change the binocular correspondence between the two retinal images. The representation mechanism is implemented with sparse coding. The control mechanism develops via reinforcement learning. For each binocular input presented to the system, the control network generates an action to control the relative angle between the two eyes, as illustrated in Fig. 1.

We use the iCub robot simulation platform [12] to generate realistic binocular visual input. The iCub robot observes a fronto-parallel surface onto which natural images have been mapped. The retinal images are generated from two cameras located at the two eyes. The cameras produce a stream of binocular stimuli at a frame rate of 50fps. We extract the central 55-by-55 pixel windows from the left and right cameras, corresponding to a visual angle of 10 degrees, to model the fovea. These windows are divided into $P=100$ overlapping 10-by-10 pixel patches, whose locations are generated by five pixel shifts horizontally and vertically. Binocular stimuli $x(t) \in \mathbb{R}^N$, $N=200$ are created by concatenating the left and right components to form a single input vector.

A sparse representation mechanism is used to encode the binocular stimuli in each patch. The data from each patch is approximated by the weighted sum of 10 basis function chosen using the Matching Pursuit algorithm [14] from a dictionary of $K=400$ basis vectors. Encoding the entire foveal window results in $P K$-dimensional coefficient vectors, which are zero except in 10 locations. We make a loose analogy between each coefficient vector and the responses of a set of disparity selective simple cells in the primary visual cortex. The $K$ basis vectors represent the binocular receptive fields of a set of $K$ simple cells that respond to input from the same visual location but with different selectivity over other dimensions such as orientation, frequency and disparity. We implement a complex cell model by spatial pooling (summing the squared coefficients) over all patches. The complex cells show the same selectivity as the simple cells, but are more position invariant. The $K$ dimensional vector of model complex cell responses is used as the input for the control network. To learn the dictionary, we adapt the basis vectors to minimize the average squared reconstruction error, where the reconstruction error is defined as the difference between the original input and the approximation, and the average is taken over all patches.

The control policy is implemented by a neural network. The output of the neural network has 11 units, which control the vergence angle between the two eyes of the robot to change by different amounts. The weights of this neural network are learned by the natural actor-critic reinforcement learning algorithm [15]. We set the reward signal of the reinforcement learner to be the negative reconstruction error of the input. Thus, the control mechanism strives to minimize the reconstruction error of the input signal by manipulating the environment so that the inputs are easier to encode. Therefore both the representation and behavioral mechanisms work in tandem to maximize the fidelity of the reconstructed input signal.

In the joint learning scenario where the representation and control policy are jointly learned, we produce a binocular input with a random disparity within a range of 2 degrees every 10 frames. Within each 10 frame sequence the control mechanism issues commands to change the relative positioning of the two eyes. If the commands are random, there would be minimal overlap between the images projected on the binocularly corresponding sections of the retina.

Fig. 1: The mapping from binocular retinal images to the motor commands. Adapted from [11].
However, under this framework, it is possible for a visually driven control strategy to emerge that maintains binocular correspondence of the left and right eye inputs by adjusting the vergence angle between the two eyes so that the left and right eye receptive fields fall on the same part of the environment.

III. RESULTS

A. Binocular correlation aligns RF orientation

Our first experiment evaluates the role of correlated binocular vision in aligning the preferred orientations of the left and right eye receptive fields.

We initialize the left and right eye components of the basis vectors as Gabor wavelets with the same wavelength and Gaussian window, but possibly mismatched orientations and phases. The standard deviation of the circular Gaussian windows is sampled from a uniform distribution between 2 and 8 pixels. The wavelength is sampled from the same uniform distribution. The phases are sampled uniformly between $\pm \pi$ and independently for each eye. The orientation angles are sampled uniformly from 0 to $\pi$ and independently for each eye. A representative sample of the basis vectors at initialization is given in Fig. 2(a).

In this first set of experiments we do not include the control of eye movements, but focus only on development of the visual receptive fields when the input disparity statistics are constant. We assume the eyes remain fixed. To model correlated visual inputs, we present the inputs such that the retinal disparities are drawn from a Laplacian distribution with zero mean and a standard deviation of one pixel (~0.2 deg.). We consider two alternative development conditions: monocular deprivation and uncorrelated binocular inputs. Monocular deprivation is modeled by replacing the right eye signal with zeros. Uncorrelated binocular inputs are modeled by setting the eye positions such that the right and left image patches do not overlap on the same part of the environment.

We evaluate the alignment of the left and right eye basis vectors after 40,000 iterations of training. Orientation tuning is obtained by fitting Gabor wavelets to the basis vectors. The left and right segments of the basis vectors are fitted with separate Gabor wavelets. Orientation difference is calculated between the corresponding right and left receptive fields, if both Gabor fits have an error less than 20% of its squared norm.

Figure 3(a) shows the histogram of the difference between the initial orientation preferences of the left and right eyes. The orientation differences are uniformly distributed due to our initialization strategy. In Fig. 3(b) we can observe that the orientation difference histogram for correlated binocular visual inputs shows a clear peak at zero, indicating that the orientations of the left and right receptive fields are aligned. On the other hand, under monocular deprivation, the distribution of orientation differences remains uniform, as shown in Fig. 3(c). This is consistent with the results of the studies by Wang et al. [8], where the distribution of orientation differences remains largely unchanged before and after the critical period. We can observe in Fig. 3(d) that under binocular uncorrelated inputs, the distribution of orientation differences also remains uniform similar to the monocular deprivation study. Therefore we can state that correlated binocular inputs are required to obtain orientation alignment in left and right receptive fields.

B. Orientation alignment under joint development

The previous experiments assumed that the left and right eyes were fixed, and that the agent was presented with the input while remaining passive. It is more realistic to assume that the agent is exposed to inputs at a wide range of depths, and controls the relative positioning of the two eyes. In this case, the agent actively controls the statistics of the visual input, which change as the eye movement control policy changes.

In order to demonstrate that the orientation alignment observed by Wang et al. in [8] still occurs under this more realistic scenario, we ran the model where the basis functions
and the policy were allowed to develop simultaneously.

Figure 2(b) shows the same set of basis vectors as in Fig. 2(a) after the joint learning of a behavioral policy and representation which strives to maximize signal fidelity. By visual inspection we can observe that the left and right orientations have aligned with each other.

To quantify this effect, we analyze basis vector properties at three time points: at initialization, after 40,000 iterations (20% of training) and at the end of the joint training. Figures 4 (a), (b), and (c) show the histograms of orientation differences at these points. At initialization (a), the distribution of orientation differences is approximately uniform. At 40,000 iterations (b), a peak at zero has started to emerge, but the majority of basis vectors are not aligned. In our first experiment, the majority of basis vectors were aligned after 40,000 iterations (Fig. 3(b)). The key difference is that the actions of the agent determine the input disparity statistics. Since a policy maintaining binocular fixation on the same point in the environment has not yet emerged, the inputs are still largely uncorrelated. The binocular fixation policy eventually does emerge, so that at the end of training (c), there is a large peak at zero, indicating that the orientations of the left and right eye basis vectors are nearly all orientation aligned.

We also analyze the disparity tuning characteristics of the basis vectors at these three time points. Disparity preference is obtained by constructing disparity tuning curves for the binocular receptive field. Tuning curves are obtained from the averaged squared response of the basis for shifted white noise patches. To create a binocular input vector, we take a 10x10 patch of white noise as the left eye input, and create the right eye input by shifting the patch horizontally by the desired disparity and fill the missing part with white noise. We calculate the average response over 10000 such samples, and normalize the resulting tuning curves to have a unit norm. Figures 4 (d), (e) and (f) show the preferred disparity of the basis vectors along with a histogram of Disparity Selectivity Indices (DSIs) of the population given as an inset. The DSI was calculated as $1 - \frac{R_{\text{min}}}{R_{\text{max}}}$ where $R_{\text{min}}$ and $R_{\text{max}}$ represent the minimum and maximum response of the tuning curve.

We classify the binocular receptive fields as disparity selective if DSI > 0.3. At initialization only 50% of the receptive fields are disparity selective. The disparity preference histogram given in Fig. 4(d) for the disparity selective units indicates that there is a large spread for the preferred disparity value. This is expected since the left and right subfields have different orientations. As training progresses, the units become more and more disparity selective. At 40,000 iterations (Fig. 4(e)), 72% of basis vectors are disparity selective. We can observe a peak at zero disparity appearing in the disparity preference histogram. At the end of training, when a control policy maintaining binocular fixation is present, the majority (92%) of the receptive fields are disparity selective. The majority of the disparity selective units are also tuned to zero disparity.

The learned control policy is visualized in Fig. 5 as an image which shows the probabilities of different eye movement actions for inputs with different retinal disparities. The 11x11 grid indicates 11 disparities and 11 actions. The gray level of each pixel indicates the probability of each action (row) given inputs at a particular disparity (column). White indicates high probability. The ideal policy which can drive the retinal disparity to zero is highlighted in green.
C. Effect of intermittent binocular alignment

As described above, given that rodents' eyes are more laterally placed than that of primates, and the experimental results by Wallace et al. [3], it is possible that rodents do not seek to maintain continuous binocular fixation. One possibility is that they alternate between binocular fusion and more independent monocular control of the eyes depending upon the environment and task demands.

In this experiment we analyze the possibility of such a system by slightly modifying our Active Efficient Coding framework. We introduce periods of independent monocular viewing for different fractions of the training time. We model independent monocular viewing by breaking the action-perception loop, and fixing the vergence angle so that the left and right eye receptive fields do not overlap on the same part of the environment. This is labeled as 'off-policy' input. We analyze the emergent properties of the receptive fields and the control policy with different fractions of off-policy independent monocular visual inputs. During periods of independent monocular viewing the sparse coding based perception sub-system is updated but since the images are generated off-policy, the reinforcement learning based controller is not updated. As a result the sparse coding mechanism evolves to represent both binocular and uncorrelated visual inputs. Uncorrelated visual inputs are best represented by monocular receptive fields, which model left and right eye inputs independently. Thus, we observe a larger fraction of monocular receptive fields as the fraction of off-policy viewing increases.

In Fig. 5(a), we compare the policy evolution with different fractions of off-policy inputs pertaining to monocular viewing along with the structure of the resulting receptive fields. The deviation of the learned policy from the ideal policy is quantified using the Root Mean Square Error between the learned and the ideal policy. Fig. 5(b) shows the percentage of disparity selective units and Fig. 5(c) shows the percentage of binocular units for the different fractions of off-policy inputs. Binocularity is measured based on the technique outlined in [16] which computes the ocular dominance histogram for the entire dictionary. Units which are placed in bin 1 and 7 in the histogram are classified as monocular and the rest as binocular. Fig. 5(a) shows that as the percentage of off-policy inputs increases, it becomes more and more difficult to learn a binocular fixation policy. If this fraction is increased to around 70%, the majority of receptive fields become monocular. In contrast, if the fraction is around 50% or lower, the learned eye movement control policy can maintain binocular fixation. Since we have previously shown that the emergence of such a control policy results in the alignment of receptive fields, we conclude that orientation alignment can occur in a scenario where the animal is alternating between independent and fusional binocular vision.

IV. Discussion

Using sparse coding to model the development of neural processing, we obtain qualitatively similar results to [8]. Our results highlight the importance of correlated binocular inputs for the orientation alignment of right and left receptive visual fields. Our results shown in Section III.A indicate that orientation alignment does not occur under either monocular deprivation or uncorrelated binocular visual inputs. It would be interesting to see if the experiment in [8] could be extended to animals with eyes that are surgically manipulated such that the binocular overlap is minimal.

In a behaving animal, the correlated binocular inputs required for orientation alignment can be obtained by controlling the gaze direction of the two eyes systematically, so that the left and right eye receptive fields to cover the same part of the environment. To model this, we extend our experiments to a more realistic scenario where the agent can actively interact with the environment using the Active Efficient Coding framework, which jointly learns both the neural representation and the agent’s behavior in the environment. We show that such a system can learn a control policy to manipulate the left and right eyes to align the two retinal images. In the process, the orientations of the left and right eye receptive fields of binocular neurons also become aligned. Although more complex models have been proposed with respect to the development of binocular receptive fields in rodents [17], our model is novel in that past models did not consider the behavior that give rise to the input statistics.

The use of a mechanism that actively controls the eyes to maintain binocular correspondence may seem at odds with the results of [3], which suggest that rodents maintain a binocular field, but not constant fusion. One potential way to resolve this discrepancy is to take into account the much lower visual acuity of rodents, which implies that the precise control
observed in primates may not be required by rodents. Rodent visual neurons have much larger receptive fields (tens of degrees) and lower spatial frequency selectivity (~0.05 cycles per degree) than primates (a few degrees/0.5 cycles per degree). Thus, only coarse control may be required to maintain the binocular alignment within the receptive field required for stereovision. Consistent with this is the finding that disparity tuned neurons in mice have a much larger disparity range than in primates [7]. Recent behavioral experiments also suggest that rats use stereovision for depth perception [18].

With somewhat laterally placed eyes with a limited binocular visual field but a larger total field of vision, there is a possibility that rodents might be alternating between two modes of vision based on the task demands. In this work we show that it is still possible to learn a control policy which facilitates the maintenance of binocular overlap under such a scheme where periods of uncorrelated visual inputs are present. It is interesting to observe that the Active Efficient Coding system is still able to learn an adequate control policy under systematic perturbations which alter the closed loop nature of the system.

Even though we see a qualitative similarity between the results produced by the original study and results produced by our Active Efficient Coding system, the orientation difference histograms obtained at the end of training have some differences. In adult mice, even though there is a clear peak in the orientation difference histogram at zero (indicating a high number of cells with matching orientations), there is a large spread of orientation difference values. With our framework, after training for a sufficiently long period, almost all (94%) of the receptive fields get aligned. The differences might emerge because the binocular visual stream generated using the iCub simulator is an oversimplification of the natural inputs generated by the mouse retina. One source for the difference might be due to the fact that we didn’t use any slanted surfaces in the training. It has been pointed out that orientation differences might be used by the visual cortex to encode slant information [19]. Furthermore, the binocular region of the mouse retina includes peripheral regions off the visual axis. This could also lead to systematic orientation differences due to imaging effects [20]. Another factor that might give rise to changes might be the limited time window where cortical plasticity is high. Primary visual cortical cells in primates and rats have a critical period for development after which further structural changes are limited, whereas in our framework, we assumed constant learning rates throughout the training.

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