Active Efficient Coding Explains the Development of Binocular Vision and its Failure in Amblyopia

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The development of vision during the first months of life is an active process that comprises the learning of appropriate neural representations and the learning of accurate eye movements. While it has long been suspected that the two learning processes are coupled, there is still no widely accepted theoretical framework describing this joint development. Here we propose a computational model of the development of active binocular vision to fill this gap. The model is based on a new formulation of the *Active Efficient Coding* theory, which proposes that eye movements, as well as stimulus encoding, are jointly adapted to maximize the overall coding efficiency of the system. Under healthy conditions, the model self-calibrates to perform accurate vergence and accommodation eye movements. It exploits disparity cues to deduce the direction of defocus, which leads to coordinated vergence and accommodation responses. In a simulated anisometropic case, where the refraction power of the two eyes differs, an amblyopia-like state develops, in which the foveal region of one eye is suppressed due to inputs from the other eye. After correcting for refractive errors, the model can only reach healthy performance levels if receptive fields are still plastic, in line with findings on a critical period for binocular vision development. Overall, our model offers a unifying conceptual framework for understanding the development of binocular vision under healthy conditions and in amblyopia.

efficient coding | active perception | amblyopia | vergence | accommodation

Despite making up only 2% of our body mass (1), our brains are responsible for 20% of our energy consumption (2). Therefore, organizing neural circuits to be energy efficient may provide a substantial evolutionary advantage. One means of increasing energy efficiency in sensory systems is to attune neural representations to the statistics of sensory signals. Based on this *Efficient Coding Hypothesis* (3), numerous experimental observations in different sensory modalities have been explained (4, 5). For instance, it has been shown that receptive field properties in the early visual pathway can be explained through models that learn to efficiently encode natural images (6, 7). These findings have extended classic results showing that receptive field shapes in visual cortex are highly malleable and a product of the organism's sensory experience (8–11).

Importantly, however, animals can shape the statistics of the sensory inputs through their behavior. This gives them additional degrees of freedom to optimize coding efficiency by jointly adapting their neural representations and behavior. This idea has recently been advanced as *Active Efficient Coding* (12, 13). It can be understood as a generalization of the efficient coding hypothesis (3) to active perception (14)(Fig. reffig:aec). Along these lines, *Active Efficient Coding* models have been able to explain the development of visual receptive fields and the self-calibration of smooth-pursuit and vergence eye movements (12, 13) as well as the development

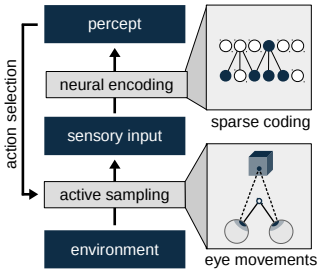

Fig. 1. The action-perception loop. The sensory input is obtained by actively sampling signals from the environment, e.g., via eye movements. A percept is formed by neural encoding which drives the selection of actions and thereby shapes the sampling process.

of the optokinetic nystagmus (15). This has been achieved by combining a sparse coding module, which learns to efficiently represent the sensory input, with simultaneous learning of, e.g., vergence or pursuit movements so as to minimize the encoding error of the sparse coding module.

A critical restriction of these previous models is that they assume an approximately constant amount of sensory information reaching each eye at any time. This assumption is invalid if, e.g., the control of accommodation is considered. For instance, if the eyes do not properly focus on the stimulus, high spatial frequencies will be lacking from the retinal images, reducing their information content.

Here we consider a novel and more general formulation of the *Active Efficient Coding* theory that solves this problem. We formalize the goal of maximizing coding efficiency as maximizing the mutual information $I(R;C)$ between the retinal stimulus representation R and the cortical representation C under a limited resource constraint. We decompose $I(R;C)$ as:

Significance Statement

Brains must operate in an energy efficient manner. The efficient coding hypothesis states that sensory systems achieve this by adapting neural representations to the statistics of sensory input signals. Importantly, however, these statistics are influenced by the organism's behavior and how it samples information from the environment. Therefore, optimal performance requires jointly optimizing neural representations and behavior, a theory called *Active Efficient Coding*. Here we test the plausibility of this theory by proposing a computational model of the development of binocular vision. The model explains the development of accurate binocular vision under healthy conditions. In the case of refractive errors, however, the model develops an amblyopia-like state and suggests conditions for successful treatment.

SE, BS and JT designed the study. SE performed the simulations and analyzed the results. LK helped to implement the suppression model. SE and JT wrote the first draft of the paper.

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$$I(R;C) = \mathcal{H}(R) - \mathcal{H}(R|C), \quad [1]$$

where $\mathcal{H}(R)$ is the (non-negative) Shannon entropy of the retinal representation and $\mathcal{H}(R|C)$ is the (non-negative) conditional entropy of the retinal representation given the cortical encoding. Maximization of $I(R;C)$ can, therefore, be achieved by maximizing $\mathcal{H}(R)$ and minimizing $\mathcal{H}(R|C)$ at the same time. We demonstrate this approach through a concrete model of the development of binocular vision including the simultaneous calibration of vergence and accommodation control.

Indeed, newborns have difficulties bringing objects into focus and cannot yet verge their eyes properly (16). Only after several months of interacting with their visual environment, they achieve accurate control of vergence and accommodation. How infants manage to self-calibrate their control mechanisms is currently unknown. Further, in certain medical conditions, the calibration of vergence and accommodation control is hindered. For example, anisometropia describes a difference in the refractive error between the eyes. If not corrected early during development, this can evoke amblyopia: a disorder of the developing visual system that is characterized by an interocular difference in visual acuity that is not immediately resolved by refractive correction. Amblyopia can be associated with a loss of stereopsis and in severe cases lead to monocular blindness (17). However, in anisometropic amblyopia stereopsis is maintained in the periphery and at low-spatial frequencies (18–20). Furthermore, vergence and accommodation eye movements are either less accurate or completely absent (21, 22).

Although there have been recent advances in the treatment of amblyopia (23, 24), existing treatment methods do not lead to satisfactory outcomes in all patients. This is aggravated by the fact that treatment success strongly depends on the stage of neuronal circuit maturation (23). When young patients are still in a critical period of circuit plasticity (11), they often recover after refractive errors are corrected, while adults mostly remain impeded (25, 26).

The above findings are all readily explained by our computational model. Under healthy conditions, it develops accurate vergence and accommodation eye movements. To find the direction of defocus the accommodation controller learns to recruit disparity information, which leads to coupled vergence and accommodation movements. In order to probe the plausibility of the model, we also test it under conditions of abnormal input. When the system is impaired due to monocular hyperopia, we observe that one eye suppresses the other and an amblyopia-like state develops. We show that this is due to the abnormal development of binocular receptive fields in the model and demonstrate how healthy binocular vision is regained when the receptive fields readapt after refraction correction. However, if the sensory encoding is no longer plastic and does not adapt to the changes in the visual input statistics, suppression prevails. Overall, our model suggests that coding efficiency may provide a unifying explanation for the development of active perception.

Model Formulation. The *Active Efficient Coding* model we propose has a modular structure. A sparse coding module learns the cortical encoding C given the retinal sensory representation of the two eyes R, while an accommodation reinforcement learning module maximizes $\mathcal{H}(R)$ and a vergence reinforcement learning module minimizes $\mathcal{H}(R|C)$ (see Eq. 1). All three modules learn simultaneously and explain the development and calibration of high fidelity control of vergence and accommodation.

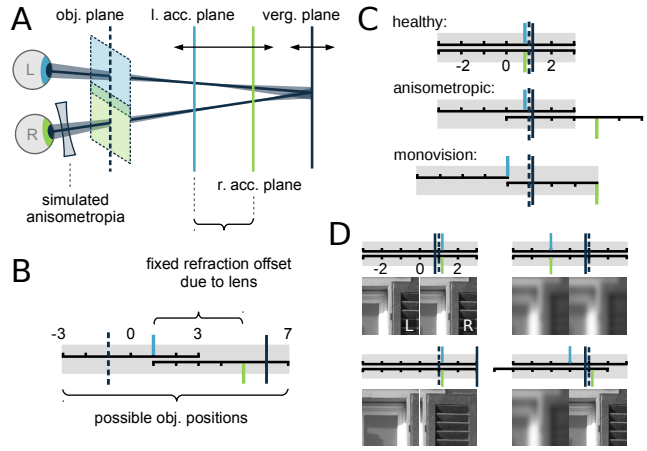

Fig. 2. Retinal input sampling from the environment. *(A)* Object position, eye focus, and eye fixation at different distances are represented as different plane positions. *(B)* Abstraction of *A*. The gray horizontal bar indicates the range where objects are presented during the simulation and also indicates the fixation range, i.e., possible vergence plane positions. Horizontal axes indicate reachable accommodation plane positions for the left (light blue) and right (green) eye. Note that when the stimulus is placed at, e.g., position 0 it cannot be focused by the right eye in this example. Accommodation and vergence errors are measured as the distance between the respective planes and the object position, in a.u.. *(C)* Position range of accommodation and vergence planes under different conditions. Same scheme as in *B*. *(D)* Examples of retinal input images for different plane position configurations. For better visibility, disparity shifts and defocus blur are increased compared to actual values.

Our model comprises an observer looking at a textured planar object. The object is sampled by the two eyes for ten subsequent iterations which constitute one fixation. After each fixation, a new object is presented at a new, random distance. The reinforcement learning modules control the retinal input by shifting accommodation and vergence planes along the egocentric axis (Fig. 2). The resulting retinal images are whitened monocularly and then binocularly encoded by a population of cortical neurons. In our model, the cortical population activity represents the binocular 'percept' from which behavioral commands are generated (compare Fig. 1, top).

At the cortical stage, we use two binocular sparse coders to efficiently encode the binocular retinal representation with a weighted set of bases: One for fine details in the foveal region and one for the periphery that receives a low-pass filtered input (see Methods). All bases are adjusted online to reflect the stimulus statistics, e.g., via their disparity and frequency tuning distributions (27) and resemble receptive fields of simple cells in the visual cortex (7) (Fig. 3, center).

We further employ a basic interocular suppression model (Fig. 4) to describe dynamic contrast modulation based on the ocular balance of the input encoding. If mostly right (left) monocular bases are recruited by the sparse coder, the contrast of the right(left) eye input is enhanced in subsequent iterations. This is in agreement with reciprocal excitation of similarly tuned neurons in visual cortex (28, 29). At the same time, the total input energy is kept balanced to ensure similar activity levels for monocular and binocular visual experience as observed experimentally at high contrast levels (30) (see Methods).

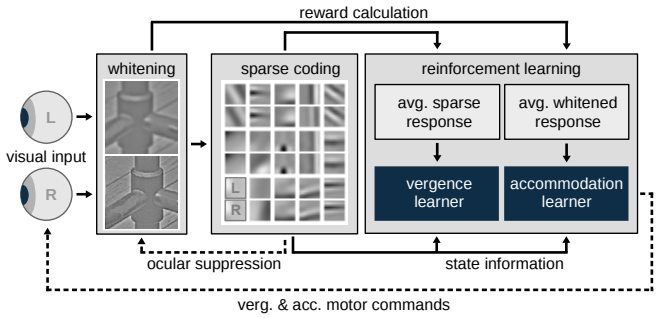

Fig. 3. Model architecture with solid arrows representing the flow of sensory information and dashed arrows representing the flow of control commands. Only one scale is shown. Sampled input images with given defocus blur and disparity are whitened (left). Thereafter, they are sparsely encoded by a set of binocular bases roughly analogous to V1 simple cells. In the healthy case, without refractive errors, receptive fields are mostly binocular and tuned to disparities near zero (center). The population-averaged sparse activity serves as state information for two reinforcement modules (right) which control vergence and accommodation commands, respectively. Accommodation commands are learned to maximize the mean squared response after whitening (avg. whitened response). The reward for the vergence learner is the negative reconstruction error of the sparse encoding stage which can be read out as the averaged squared sparse response (see Methods).

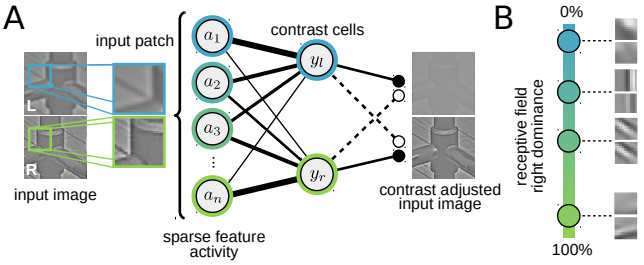

Fig. 4. Interocular suppression model. *(A)* When mostly right(left) monocular feature bases a_j are used to encode an input patch, the right(left) contrast cell $y_r(y_l)$ becomes activated and the left(right) retinal image is suppressed. Dashed(solid) lines indicate inhibitory(excitatory) interactions. Connection strength is represented by line thickness. We model interocular suppression to be scale specific, i.e., when the foveal region of the left eye is suppressed, the periphery of the left eye may still provide unattenuated input (see Methods for details). *(B)* Binocularity of five bases; from mostly right monocular (green) to almost exclusively left monocular (blue).

Maximizing the entropy of the retinal response $\mathcal{H}(R)$ (Eq. 1) with the accommodation reinforcement learning module lets the system favor inputs with high spatial frequencies. This is due to the edge-enhancing nature of retinal ganglion cell receptive fields. With their center-surround receptive fields, they are selective for sharp contrasts and respond poorly when out of focus input is presented. Their receptive field shape has also been interpreted as a result of maximizing coding efficiency (6, 31). We assume the spatial frequency tuning of retinal ganglion cells to be static and thus independent of the distribution of spatial frequencies in the retinal input as suggested by deprivation experiments (10, 32, 33).

The conditional entropy $\mathcal{H}(R|C)$ (see Eq. 1) can be understood as the information that is lost, i.e., not encoded, at the cortical stage. By minimizing lost information the second reinforcement learning module that controls vergence behavior (Fig. 3) favors stimuli with highly correlated left and right eye inputs. Both terms in [1] can be approximated with the average population activity at the cortical and retinal stage, respectively (Fig. 3) (see Methods). Thus, vergence and accommodation controllers jointly maximize sensory coding efficiency.

Results

Active Efficient Coding Leads to Self-calibration of Active Binocular Vision. In the healthy condition without refractive errors and with coinciding left and right accommodation planes (Fig. 2*C*, top), the model learns to perform precise vergence eye movements (Fig. 5*A* and *B*) while most neurons develop binocular receptive fields (Fig. 3, center and Fig. 7*B*). Accommodation performance is highly accurate as well. This is achieved without obvious sign cues: defocus blur changes linearly independent of whether an eye focuses behind or in front of the object (SI Appendix, Fig. S1). Also, neither chromatic (34) nor other higher order aberrations (35) are provided in our model, which could help to steer focus in the right direction. Instead, we found that input disparity is utilized to shift focus in the correct direction (SI Appendix, Fig. S3, bottom row). The system capitalizes on the simultaneous movement of the vergence and accommodation planes such that the sign of defocus is inferred from disparity cues (SI Appendix, Fig. S3).

Model correctly describes response to unnatural visual input. The impact of input disparity on the accommodation policy that was trained under healthy conditions becomes even more apparent when 'unnatural' input is presented. We placed virtual prisms in front of the eyes, which changed the vergence target distance while the accommodation target distance remained unaltered (Fig. 6*A*). In response, accommodation focus erroneously shifted in the direction of the new fixation target plane. Removing the prisms, we observed the same effect in the opposite direction. This is in accordance with experiments (36) and can lead to visual fatigue and discomfort while using virtual reality headsets (37).

We also examined the short-term effect of lens-induced anisometropia. By introducing a refractive error to one eye, the left and the right accommodation plane are now separated such that only one of the retinal images can be in focus at any given time (Fig. 2*C*, center). As was previously suggested (38), when we present a stimulus moving in small steps the system chooses to continuously focus with one or the other eye dependent on the initial stimulus position (SI Appendix, Fig. S4). However, when objects are positioned at random distances both eyes are alternately prioritized to focus the object (Fig. 6*B*). In accordance with experimental data (38), vergence performance was slightly decreased compared to the healthy case.

Anisometropia drives model into amblyopic state. To test how the model evolves under abnormal rearing conditions, we simulated an anisometropic case by adding a simulated lens in front of the right eye such that it became hyperopic and was unable to focus objects at close distances (Fig. 2*C*, center). Different from the healthy case where neither of the eyes is favored over the other, in the anisometropic case an amblyopia-like state emerges. Foveal input from the hyperopic eye becomes actively suppressed (SI Appendix, Fig. S2*C*) while the peripheral input is unaffected and still provides binocular information such that a coarse control of vergence is maintained (Fig. 5*A* and SI Appendix, Fig. S2*B*). This results in stable binocular receptive fields in the periphery which provide enough information for coarse stereopsis as observed in experiments (18–20).

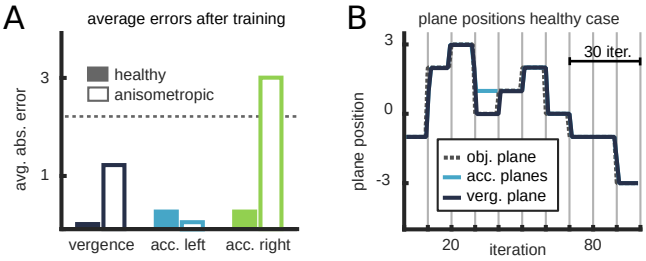

Fig. 5. Model performance under healthy and anisometropic conditions. *(A)* Average absolute vergence and accommodation errors after training under healthy and anisometropic conditions. The dashed line indicates the expected average vergence error if accommodation planes are moved randomly under healthy conditions. *(B)* Example trajectories of plane positions after training under healthy conditions (left and right acc. plane coincide - Fig.2*C*, top). Shortly after the start of a new fixation where stimulus distance and image are randomly switched (vertical gray lines) all planes overlap at the object distance (dotted line).

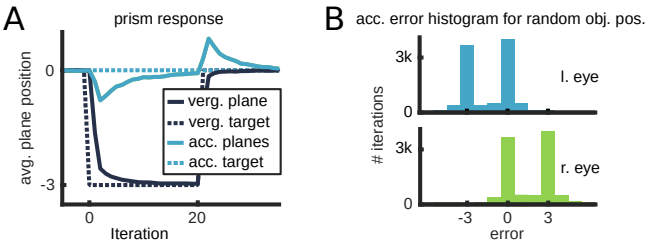

Fig. 6. Vergence-accommodation coupling after training under healthy conditions. *(A)* Average vergence and accommodation plane trajectories while adding and removing additional lenses at iteration 0 and 20, respectively. Target planes which yield zero disparity (dark blue) and zero blur (light blue) are shown as dotted lines. *(B)* Accommodation error histogram of model trained under healthy conditions and tested under lens-induced anisometropia for random object positions.

Accommodation adapts such that the stimulus is continuously tracked with the unimpaired eye (SI Appendix, Fig. S5).

Early but not late refractive correction rescues binocular vision. To test if the anisometropic model can recover from amblyopia upon correction of the refractive error, we first trained a fully plastic system under anisometropic conditions until it reached stable performance. Then, all refractive errors were corrected. When the receptive fields were fixed after the refractive error was corrected, receptive fields remained monocular and the system did not recover from the amblyopic state. Instead, it maintained a high level of vergence error (Fig. 7*A*, dotted line). In contrast, when receptive fields remained plastic and could adapt to the changed input statistics weak responses of the formerly impaired eye were restored to larger values (Fig. 7*A* and SI Appendix, Fig. S6), solid lines). This was due to a shift from monocular to binocular receptive fields as a result of the changed input statistics (Fig. 7*B*). This is in line with a large body of evidence suggesting that limited cortical plasticity prevents recovery from amblyopia after the correction of refractive errors (11, 23, 24).

Unbiased Anisometropia Evokes Monovision. We wondered if an amblyopia-like state would also develop if both eyes were similarly impaired but with opposite sign of the refractive error. We adjusted the parameters such that the left eye was myopic and the right eye hyperopic. Objects were placed between the minimum focusable position of the myopic eye and the maximum focusable distance of the hyperopic eye (Fig. 2*C*, bottom). This configuration is similar to monovision, a treatment method for presbyopia where the ametropic condition is achieved via optical lenses or surgery (39). In such cases, the relatively more myopic eye is used for near and the relatively less myopic eye for distant vision. Thereby, the required amount of accommodation is reduced. In our model we observe the same effect (SI Appendix, Fig. S7*A* and *C*). Neither of the two eyes is suppressed permanently, although foveal receptive fields are mostly monocular. Rather, when distant objects are focused the myopic eye is suppressed and when close stimuli are presented the hyperopic eye is suppressed. When either one of the eyes could be utilized to focus on a stimulus, hysteresis develops, i.e., when the left eye was suppressed in the previous fixation the right eye tends to be used to focus and vice versa (SI Appendix, Fig. S7*B*).

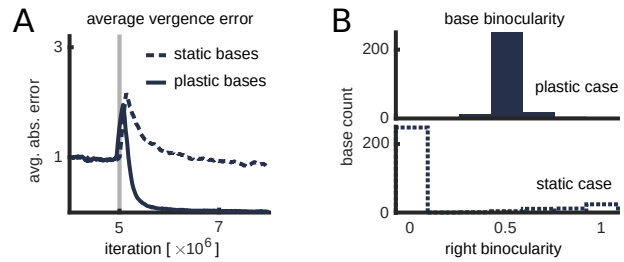

Fig. 7. Model performance after refractive correction. *(A)* Vergence performance of formerly anisometropic systems after correction of all refractive errors at iteration 5×10^6 (vertical gray line). The (dotted)solid line indicates system with (non-)plastic receptive fields. The initial increase in the vergence error is due to the required recalibration of the reinforcement learning module. *(B)* Histogram of foveal receptive field binocularity $b_{(\cdot,r)}$ after refractive error correction (see Methods for details).

Discussion

We have shown how optimizing both behavior and encoding for efficiency leads to the self-calibration of active binocular vision. Specifically, our model, which is based on a new formulation of the *Active Efficient Coding* theory, accounts for the simultaneous development of vergence and accommodation. Under healthy conditions, the model develops accurate vergence and accommodation eye movements. For a simulated anisometropia, however, where one eye suffers from a refractive error while the other eye is unaffected, it develops into an amblyopia-like state with monocular receptive fields and loss of stereopsis. Recovery from this amblyopia-like state is only possible if receptive fields in the model remain plastic, matching findings of a critical period for binocular development (11). Furthermore, when the eyes have opposite refractive errors, a form of monovision develops, where the myopic eye is used to focus near objects and the hyperopic eye is used for distant objects. Thus, the model explains a range of findings from a unified computational perspective of coding efficiency.

While we have focused on the development of active binocular vision including accommodation and vergence control, our formulation of *Active Efficient Coding* is very general and could be applied to many active perception systems across species and sensory modalities. *Active Efficient Coding* is rooted in classic efficient coding ideas (3–7), of which predictive coding theories are special examples (40–42). Classic efficient coding does not consider optimizing behavior, however. Friston's Active Inference approach does consider the generation of behavior in a very general fashion. There, motor commands are generated so as to fulfill sensory predictions.

In our new formulation of *Active Efficient Coding*, motor commands are learned to maximize the mutual information between the retinal response and its cortical representation. This implies maximizing the amount of sensory information sampled from the environment and avoids the problem of deliberately using accommodation to defocus the eyes (or closing the eyes altogether) to make the sensory input easy to encode and/or predict. As such, our approach is more related to Schmidhuber's ideas on maximizing compression progress (43).

Interestingly, during training, the model learns to exploit disparity cues for determining the direction of defocus. This leads to a coupling of vergence and accommodation as observed experimentally (44) and neurally (45). Humans are believed to use additional sign cues for determining the direction of defocus (34, 35, 44). We deliberately excluded such cues from the model to emphasize the fact that they are not strictly necessary to learn accurate accommodation control under otherwise healthy conditions. Investigating how such additional cues might affect our model is left for future work.

Other aspects of our model are also greatly simplified compared to biology. An important example is the inter-ocular suppression mechanism. The simple logic behind the used suppression mechanism is that every "neuron" tries to maximize its own activity by suppressing competing input from the other eye. This proved sufficient to account for the development of an amblyopia-like state, with mostly monocular receptive fields in the representation of the fovea. More sophisticated suppression models could be incorporated in the future (46, 47), but we do not expect them to change the conclusions from the present model. However, a topic of current interest is how suppression develops during disease and treatment, e.g., with the standard patching method. A better understanding of the role of suppression in amblyopia could lead to improved therapies in the future.

Interestingly, other developmental disorders such as Down syndrome or autism also affect visual development(48, 49). Specifically, both disorders are associated with reduced accommodation performance, but the underlying neural circuit mechanisms are unclear. Our model may provide a useful starting point for theorizing about deficits in accommodation control in these disorders.

Materials and Methods

Retinal Image Rendering. We used 300 grayscale converted natural images of the 'man-made' category from the McGill Database (50). One image was presented at a random position (see Fig. 2*A* and *B*) during one fixation, i.e., 10 subsequent iterations, before the next image and position were randomly selected for the next fixation. Two foveal images of size 72×72 pixels were cropped from the center of the original image and normalized to zero mean and unit variance intensity. For every distance unit between vergence and object plane, the left(right) foveal window was shifted 1px to the left(right). A Gaussian blur filter was applied to the left and the right eye image where the standard deviations depended linearly on the distance between object and accommodation planes. 1 a.u. distance equals 0.8 px of standard deviation (SI Appendix, Fig. S2C). Errors were measured in a.u. as distances to the object plane. For a second, peripheral scale the original images were downsampled with a Gaussian pyramid by a factor of 2 and again, two 72×72 px windows were extracted. Disparity and defocus blur were applied accordingly.

Input processing. The left and right retinal input images were whitened as described by Olshausen and Field (7), independent of accommodation or vergence. Retinal images were cut and merged into 121 binocular patches of size 16×8 px. Image patches were normalized to zero mean and unit variance intensity and subsequently sparsely encoded with the matching pursuit algorithm (51), where we recruited $n = 10$ out of 300 bases ϕ_i from the dictionary in order to reduce the reconstruction error $||\Phi_n||^2$, i.e., the energy of the residual after n iterations. Here, $||\cdot||$ is the Euclidean norm.

$$\Phi_n = \Phi_0 - \Phi_n^{(s)} \equiv \Phi_0 - \sum_{k=1}^{n} \alpha_{i_k} \phi_{i_k},$$

$$\alpha_{i_j} = \langle \phi_{i_j}, \Phi_{j-1} \rangle, \quad i_k = \underset{j}{\operatorname{argmax}} \left(\langle \phi_j, \Phi_{k-1} \rangle \right),$$

where Φ_0 is the normalized input patch, $\Phi_n^{(s)}$ is the sparsely encoded image patch, and α_{i_k} are the respective base activities. Foveal and peripheral scale were encoded separately by their own sparse coders and dictionaries.

Reinforcement Learning. We used two separate natural actor critic reinforcement learners (52) as presented in (13) to control the accommodation planes and the vergence plane, respectively. The plane positions can be changed in steps of [-2, -1, 0, 1, or 2] (compare Fig. 2). The state information for both reinforcement learners are the patch-averaged squared responses of the foveal and the peripheral scale bases of both matching pursuit dictionaries. The reward for the vergence learner is the negative reconstruction error of the matching pursuit algorithm, i.e., the average squared response of the base activity after patch encoding averaged over pixel values, patches, and scales. The reward for the accommodation learner is the average absolute squared pixel value of the whitened binocular image. Both rewards were normalized online to zero mean and unit variance intensity.

Maximizing Mutual Information. Rewards for the reinforcement learners are the average response after whitening and encoding, respectively. Together these can be understood as an empirical estimate of the mutual information between the whitened Φ_0 and sparse response $\Phi_n^{(s)}$:

$$I(\Phi_0, \Phi_n^{(s)}) = \mathcal{H}(\Phi_0) - \mathcal{H}(\Phi_0 | \Phi_n^{(s)}),$$

where the conditional entropy $\mathcal{H}(\Phi_0|\Phi_n^{(s)})$, is closely related to the reconstruction error, i.e., the average information in the retinal image that is not encoded at the cortical stage (see SI Appendix). In terms of the sparse coding algorithm, this corresponds to the average energy of the residual image $||\Phi_n||^2$. We make use of the 'energy conservation' property of the matching pursuit (51) which holds if we can assume that the n dictionary elements recruited for encoding are pairwise orthogonal:

$$-||\Phi_n||^2 = -||\Phi_0||^2 + \sum_j |\alpha_j|^2.$$

Since the input energy $||\Phi_0||^2$ does not depend on vergence for isotropic input statistics and is normalized to unity, we take the energy of the sparse response as the reward for the vergence learner.

For the accommodation learner, we maximize an estimate of the variance of the retinal response, i.e., $||\Phi_0||^2$. This is equal to maximizing a lower bound on the entropy which holds for a large class of unimodal distributions (53):

$$\mathcal{H}(\Phi_0) \geq c_1 \ln\left(\sigma_{\Phi_0}^2\right) + c_2,$$

where $c1$ and c_2 are positive constants. The whitening filter results in a unimodal distribution and its response distribution is close to a Laplace distribution, in which case the lower bound becomes exact (SI Appendix, Fig. S8). Therefore, by maximizing the variance, we maximize a monotonic function of a lower bound of the entropy.

Together, this leaves us with the energy of the whitened response for the accommodation reward and the energy of the sparse response for the vergence reward.

Suppression Mechanism. The suppression mechanism adjusts the contrast of left and right input image (see Fig. 4). We calculated the binocularity index of neuron i as

$$b_{(i,c)} = \frac{||\phi_{(i,c)}||}{||\phi_{(i,c)}|| + ||\phi_{(i,\bar{c})}||}, \quad c \in \{l, r\},$$

where $\phi_{(i,c)}$ is the monocular receptive subfield of neuron i. The current activity of encoding neurons was weighted with their binocularity indices and subsequently passed through the non-linearity of a contrast neuron:

$$\tau \frac{\mathrm{d}x_c}{\mathrm{d}t} = -x_c + \sum_i a_i^{(t)} b_{(i,c)},$$
$$y_c^{(t)} = \frac{s}{1-\theta}[x_c^{(t)} - \theta]_+.$$

We chose the threshold $\theta = 0.6$ and the saturation $s = 0.8$. Finally, the input patches for the sparse coder were adjusted to

$$\Phi_c^{(t+1)} \to \Phi_c^{(t+1)} \left(1 + y_c^{(t)} - y_{\bar{c}}^{(t)}\right) \equiv \Phi_c^{(t+1)} \left(2 - s_c\right),$$

where we defined the suppression factor s_c (compare SI Appendix, Fig. S6). There were two separate suppression mechanism, one per scale.

Software and Documentation. Documented MATLAB® code of the model will be made available after publication

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