Formation of Orientation-Selective Receptive Fields and Learning of Field Orientations in Realistic Environments Using Sensory-Invariant Driven Action (SIDA)
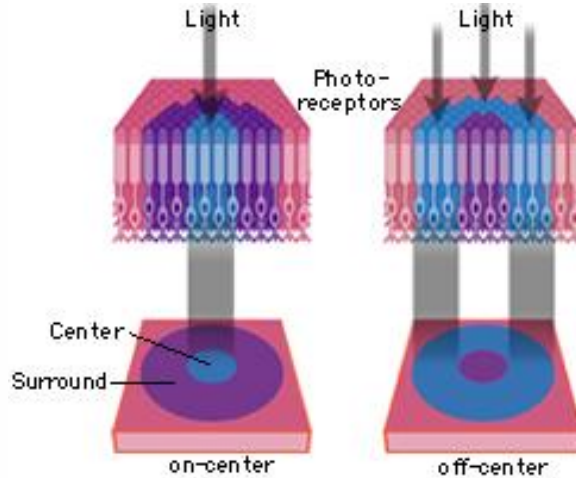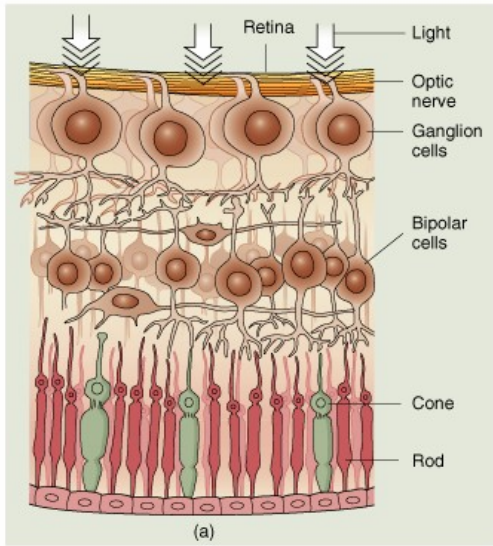
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ABSTRACT   Neurons in the visual cortex develop receptive fields that are sensitive to oriented features in the visual environment. However, exactly how these features develop in a self-organizing way, and how the brain learns to recognize what orientation is represented by a particular neuron, is not clearly understood. Explanations for the development of orientation-selective receptive fields such as ICP, PCP, and BCM theory rely on statistical analysis of visual data that is presented in a random or ordered fashion. However, it is unclear how these rules may be implemented biologically. We found that orientation-selective receptive fields might be developed from bitmap images under simpler learning rules if the action moving the gaze is considered, by analyzing the change in sensory stimulation related to movement in an attempt to maintain sensory-invariance. Because the spatial property of the action that maintains sensory invariance directly reflects the feature encoded by the orientation-sensitive receptive field, sensory-invariance driven action (SIDA) may provide a better basis for conceptualization and learning of receptive fields than previously proposed models. SIDA has already been used to explain the learning of orientation preferences by the brain post-feature development by Choe & Bhamidipati under discrete conditions, and we also extend upon this to show how SIDA can be used to learn developed orientation-preferences under continuous conditions from natural images.

1. PHYSIOLOGICAL INTRODUCTION TO RECEPTIVE FIELDS

Light entering the eye is focused onto the inner layer of the back of the eye by the lens. This layer, the retina, has three principal layers. Radiating outwards, they are the Ganglion cell layer, the Bipolar cell layer, and the Rod and cone cell layer. The retina is largely transparent, and light focused on the retina is first detected by the rods and cones in the back layer after passing through the first two layers. The rods and cones are individually receptive to very small points in the visual field, and define the lowest level of perceptible visual information. Activation of these cells is relayed through the Bipolar cell layer to the Ganglion cell layer. Thus, Ganglion cells have receptive fields that are composed of the photoreceptors. The Bipolar cell layer has organized lateral connections which serve to inhibit the response in the Ganglion cell layer, reducing and fine-tuning the receptive field into center-surround patches.

(a)   (b)

Fig. 1 (a) Cross-section of the retina (the inner layer of the eye), showcasing the three principal layers, with the topmost layers representing the most radially inward. Light passes through the Ganglion and Bipolar layers before being detected by the rods and cones (photoreceptors), which propagate the signal back through the Bipolar layer to the Ganglion cell layer via action potentials. (b) An abstracted image showing the two kinds of center-surround receptive fields of individual Ganglion cells as composed by excitatory and inhibitory dendritic connections from photoreceptors and Bipolar cells. Figures taken from John Wiley & Sons & BrainConnection.com.

The Ganglion cells then propagate this information to the thalamus via the optic tract by sending action potentials, where it is propagated through the ventral / dorsal thalamus (LGN) and to the first layer of the primary visual cortex (V1).
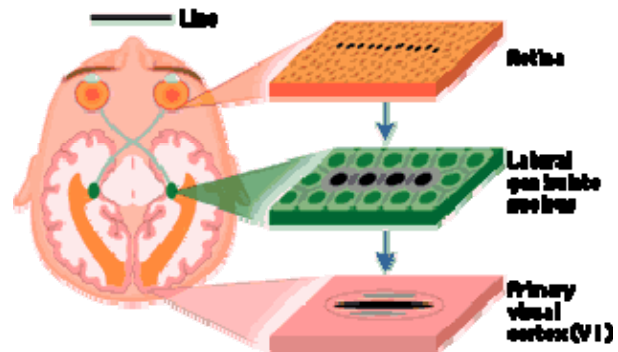

Fig. 2 Simplified image showing how neurons in V1 have orientation-selective receptive fields. A line in the visual field causes photoreceptors in a linear organization to be stimulated, which stimulate Ganglion cells in a linear organization. The activated Ganglion cells send signals into the thalamus, through the Lateral Geniculate Nucleus (LGN), and strongly stimulate a neuron in the visual cortex that has strong synaptic weights to all of the neurons carrying the incoming signal. Figure taken from BrainConnection.com.

Thus, neurons in V1 have receptive fields composed of individual Ganglion cell receptive fields. By presenting test subjects with various

images in various locations and measuring the activation of neurons in the subject's brain, the receptive fields of V1 neurons have been measured, and many of them are selective to lines of certain orientations.
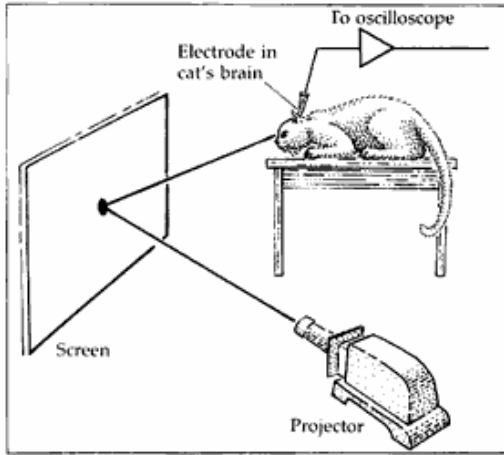

Fig.3 An electrode measures the response of a single neuron in V1 while visual stimuli is presented to the subject on the screen. By determining the areas of the screen where light excites (increases the firing frequency of the neuron) and inhibits (reduces the firing frequency), the receptive field of the neuron can be mapped.
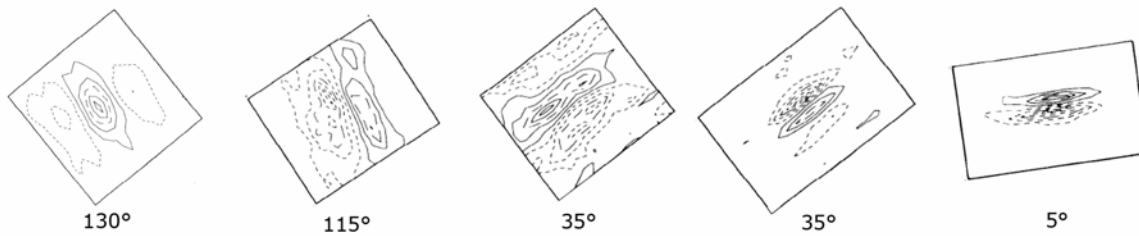

Fig. 2 Examples of individual neuron receptive field feature maps in cat striate cortex, and their orientation selectivity. Solid isolines represent positively stimulated regions, while dotted isolines represent negatively stimulated regions. Cross-sections of the field map perpendicular to the angle of orientation-selectivity resemble a Gabor function, with alternating positively and negatively stimulated regions decaying in intensity from the center. Figures taken from Jones & Palmer (1987).

There are many neurons with different orientation-selective receptive features that map to tightly overlapping areas in the visual field, allowing for a line of any orientation at any coordinate in the visual field to stimulate some neurons in V1. Interestingly, the mapping of receptive fields in V1 to the visual field is nearly topographical, in that the relative position of neurons in V1 roughly corresponds to the positions of their receptive fields in the visual field.
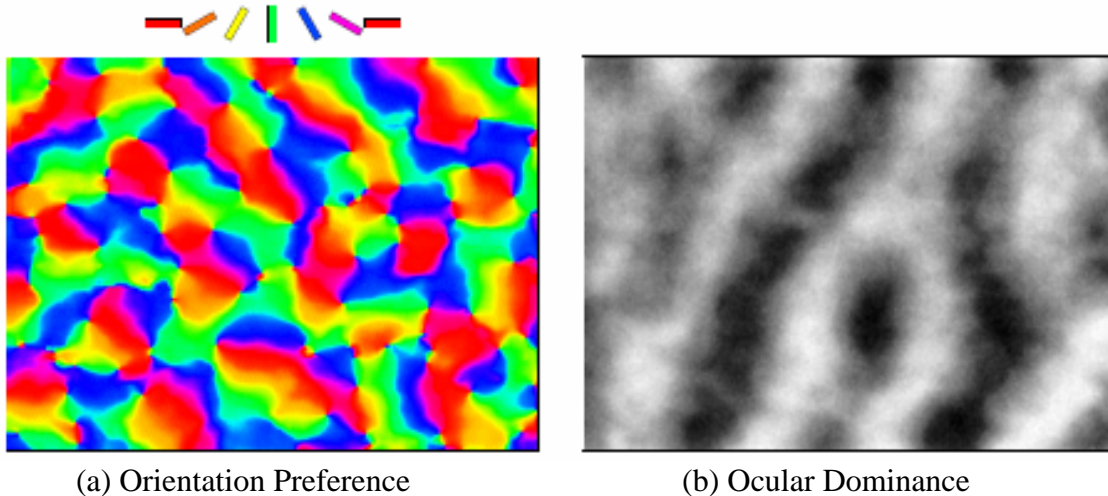
(a) Orientation Preference   (b) Ocular Dominance

Fig. 3 (a) This color map indicates patches of overlapping orientation sensitivity measured in a 4mm x 3mm patch of the cortical surface in a macaque monkey. (b) Ocular dominance map of the same area on the cortical surface, showing how strongly the cells prefer input from the left (white) vs. right (black) eye. Figure borrowed from Computation Maps in the Visual Cortex (2004).

The neural processes in the brain may perform some kind of edge-detection pre-processing on visual information, allowing the orientation-selective V1 neurons to be supplied with edge information rather than pure image information. Based on the map of stimulated V1 neurons and the knowledge of what orientation each neuron is selective for, the outlines of shapes in the visual field can be reconstructed, which may be how the brain is able to form mental images.

The synaptic connections between neurons in the retina, thalamus, RTN and visual cortex are all dynamically mutable. Since it is the sum of these synaptic connections that determine a neuron's receptive field, receptive fields are therefore changeable.

Receptive fields mostly form during the early stages of development, and are greatly influenced by the environment. For instance, kittens raised in environments lacking lines of certain orientation will be inept at recognizing lines of that orientation – suggesting that they lack orientation-selective neurons for those orientations. However, it has also been shown that some rudimentary receptive features have already been formed before the eyes are opened. These may be explained by retinal waves or PGO waves.

2. MOTIVATION

Theoretical models for receptive field formation exist, mostly using independent component analysis or principal component analysis. All of these models are based on random samplings from visual fields and analyzing them to find the independent orientation components. However, it is unclear what kind of rules individual neurons might follow to bring about this kind of behavior as a whole.

Additionally, all of the current methods ignore the order that images are sampled in, and hence the action of the eye. We believe that action (movement of the eye's focus) may play an important role in the development of these receptive fields, and that by considering the action, contextual information may be gathered that is used in receptive field formation.

Also, existing receptive field formation theories do not provide any means for the brain to

recognize the orientation represented by a developed receptive field, and this must be accomplished before the brain could meaningful interpret sensory data. Experiments with kittens have shown that voluntary action is necessary for visual learning, which may be because without voluntary action the orientation-preferences of neurons cannot be learned, or because the method that the brain uses to develop receptive fields relies on active motion.
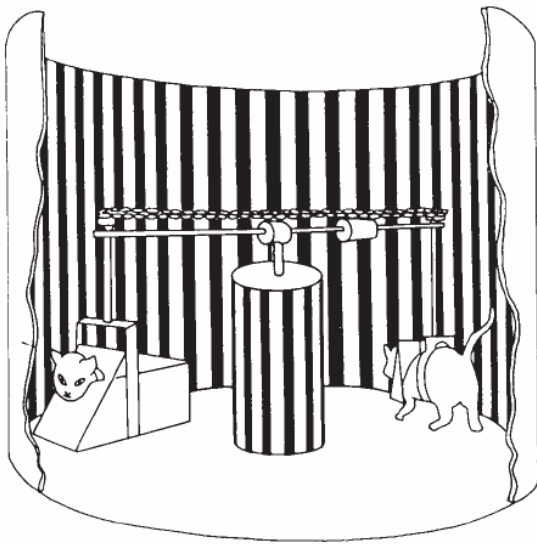

Fig. 4. Experiment by Held and Hein in which two kittens are attached to a carousel, and one can move and the other cannot. Both kittens receive the same visual stimulation, but only the one that is actively moving develops normal sensory-motor coordination. Figure taken from Granlund (1999).

3. METHODS

In order to test the effect of action, we used a driver algorithm to traverse the natural image after using convolution filters to detect the edges. This driver algorithm operated based on four simple rules: 1) maximize the stimulation of the most stimulated neuron's receptive field, 2) attempt to maintain sensory invariance by having the same neuron's receptive field be stimulated repeatedly if possible, 3) try to move in the straightest path possible, 4) periodically

find a new area of interest after some number of iterations.

Receptive fields in our model are represented by grayscale bitmap images, where individual pixel intensities represent the strength of the synaptic weight to the Ganglion cell that has a receptive field centered at that relative position.

To simulate receptive field formation, we originally assigned random noise patterns to bitmap images representing the receptive fields of each neuron. Then we used the driving algorithm to traverse the convolved image and find sample points, and the receptive fields were trained to match the visual field at the training points using Hebbian learning.

For each training point, only the most stimulated neuron was trained (training all fields relative to the stimulation level would eventually result in convergence of receptive fields). The stimulation of each neuron in our model is largely dependent on the "age" of the neuron, measured by the number of Hebbian training iterations (morphs) that have been done on that neuron's receptive field.

We found that using a superposition of decreasing exponentials for the basic function worked well; the first exponential provides a brief initial period of heightened stimulation which allows for rapid diversification so that each receptive field quickly assumes a feature mimicking the visual field, and the second exponential provides a damping force that allows the fields to stabilize over time, allowing each receptive field to represent a specific orientation that can be learned rather than continuously mutating orientation preferences.

The stimulation function of a receptive field is given by

$$S = \sum_{p=0}^{P} \left(\frac{p}{255} - \frac{v}{255} \right) \left(\sigma \cdot e^{\left(-\frac{m}{\alpha}\right)} + e^{\left(-\frac{m}{\beta}\right)} + z \right), \qquad [1]$$

where P is the number of pixels in the receptive field image, and p is the pixel index in the receptive field. v is the pixel index of the visual field that corresponds to p. m is the number of morphs (the number of Hebbian training iterations that have been run on this RF). The factors of beta and alpha control the rate of sensitivity decay, where beta > alpha. Alpha is a factor that weights the initial stimulation exponential higher, and Z is the stable-state stimulation factor.

The Hebbian learning function of a pixel in the receptive field, applied to all pixels in the receptive field for one training iteration, is given by

$$R_{t=T} \leftarrow R_{t=T-1} \cdot (1 - \sigma S) + V(\sigma S), \qquad [2]$$

where R is a pixel in receptive field, and V is the pixel in the visual field that corresponds to R. S is the stimulation level of the receptive field. Sigma is a factor that dramatizes the results of training.

In order to learn the orientation of a neuron, the basic principle is assumed that it is more common to encounter repeating lines if the action is parallel to that line. As the focus point traverses the visual field, the sensory-invariance factor is continuously measured.

Neurons that maintain high sensory invariance in a particular direction of movement are adjusted so that their perceived angle matches that direction of movement. If they maintain substantial sensory-invariance in more than one direction, the weighted average of these

directions is computed to find the perceived orientation.

We found that a Hebbian training algorithm was not sufficient for learning this problem, because the sample points are path dependent, and it is possible to train for a long stretch on misrepresentative data. We found a much more reliable method was to keep track of all the information in a deformable weight space, allowing all the pertinent information from an arbitrary amount of data to be stored in a finite storage space.

The orientation space [0-360] is divided into N equal sections. Whenever the driver makes an action with angle a, the sensory-invariance of this action is added to the value in the appropriate orientation section.

The sensory-invariance factor is given by

$$\varphi = \alpha \cdot s[0] \cdot s[1], \qquad [3]$$

where s[x] is the stimulation level of the neuron's receptive field x steps into the past. Thus, s[0] is the current stimulation level and s[1] is the previous stimulation level. Alpha is an arbitrary scaling factor.

The perceived orientation of any neuron is then computed based on this orientation space. First, the weight sum (S) is computed by

$$S = \sum_{n=0}^{N} \left(\frac{P(n)}{C(n)} \right), \qquad [4]$$

where P(n) is the value in the orientation space of the nth section, and C(n) is the number of sample values that have been added into the nth section.

Then, the perceived orientation (O) is the weighted average of all of the sections meeting the minimum threshold contribution (k),

multiplied by the central angle of that section (D). The equation is given by

$$O = \sum_{\frac{P(n)}{C(n) \cdot S} > \kappa}^{N} \frac{P(n)}{C(n) \cdot S_2} \cdot D(n), \qquad [5]$$

where P(n) is the value in the orientation space of the nth section, C(n) is the number of sample values that have fallen within the nth section. S is the weight sum of all sections, S_2 is the weight sum of all sections where the threshold condition k is satisfied. D(n) is the central angle of an orientation section.

4. RESULTS

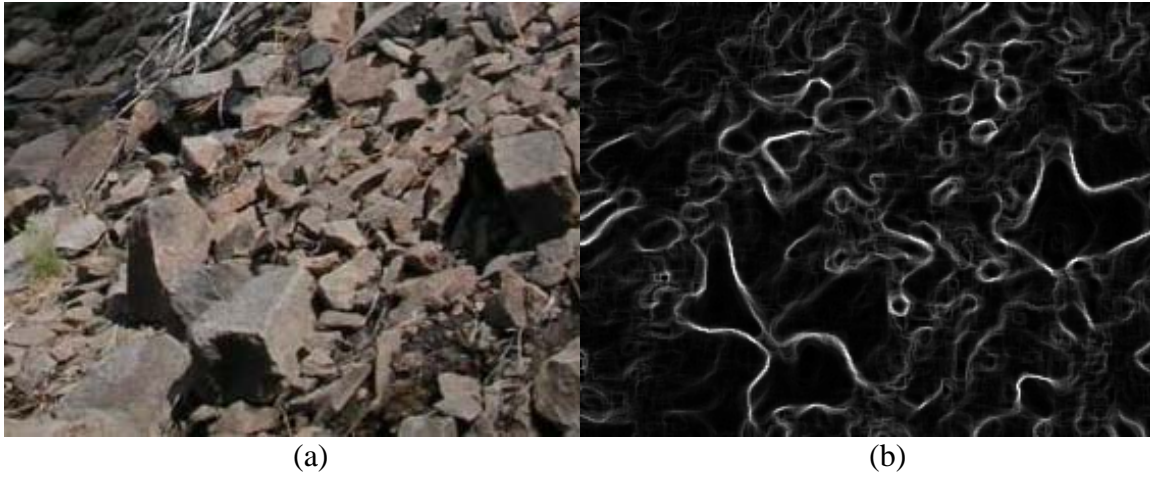<center>(a)   (b)</center>

Fig. 5. (a) This natural image of a rock-pile was used for training of receptive field formation and perception of orientation-selectivity. The black and white image in (b) is the result after pre-processing the image through a convolution filter to detect edges, and is the actual map that was used for training.
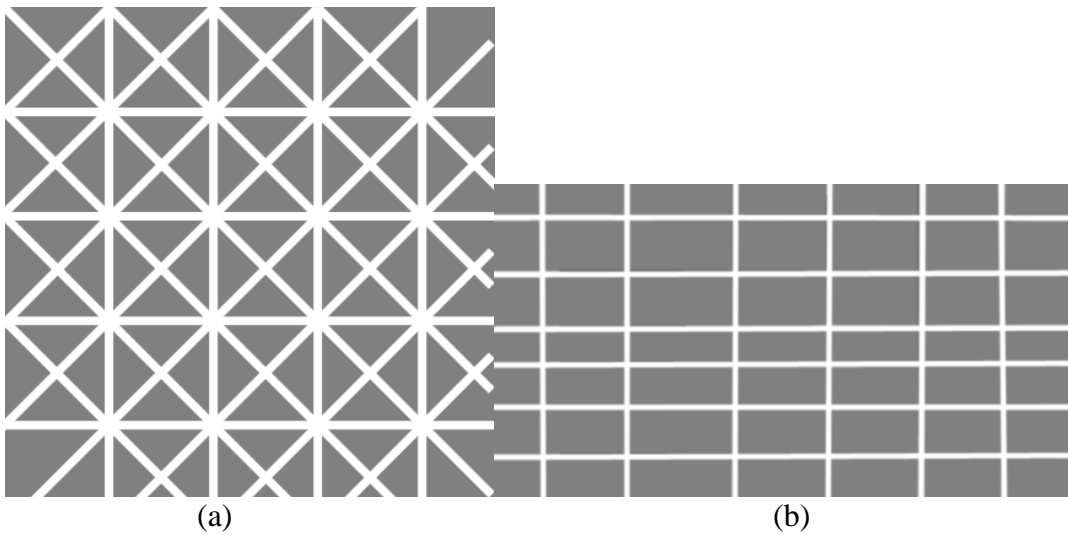

<center>(a)   (b)</center>

Fig. 6. These grayscale images were used for theoretical testing, taking the place of a convoluted real image. They were used to test the theory of perceiving receptive field orientation by correlating sensory-invariance and motion.

(a)
374 Morphs
(b)
438 Morphs
(c)
364 Morphs
(d)
375 Morphs
(e)
449 Morphs

Fig. 7. Resultant receptive feature maps after 2000 training iterations on the image in Fig. 5, without using the sensory-invariant driver. Focus points were selected randomly each iteration. Orientation-selectivity is apparent in fields (b) and (e), but not in the other fields.
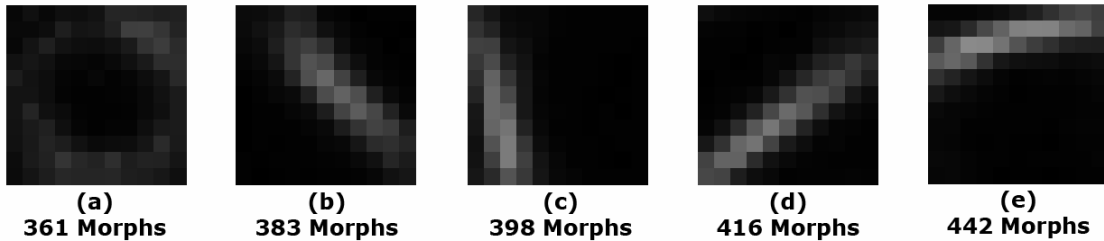

(a)
361 Morphs
(b)
383 Morphs
(c)
398 Morphs
(d)
416 Morphs
(e)
442 Morphs

Fig. 8 Resultant receptive feature maps after 2000 iterations on the image in Fig. 5, using a sensory-invariant driving function to sample the image. Orientation-selectivity with very good sparsity is apparent in all fields except for field (a), which demonstrates a vague circular pattern.
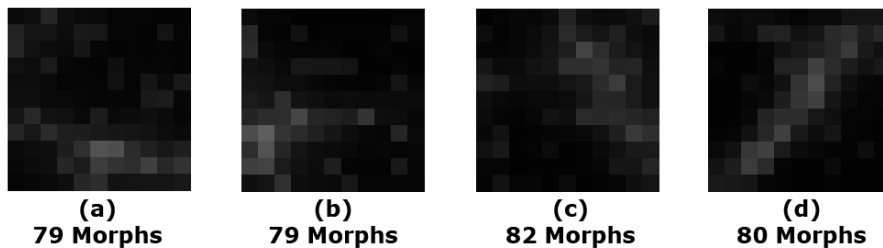

(a)
79 Morphs
(b)
79 Morphs
(c)
82 Morphs
(d)
80 Morphs

Fig. 9 After 320 iterations without using a driving function, the resulting feature maps are scrambled and only vaguely suggest orientation selectivity in some cases. Training was done on the image in Fig. 5.
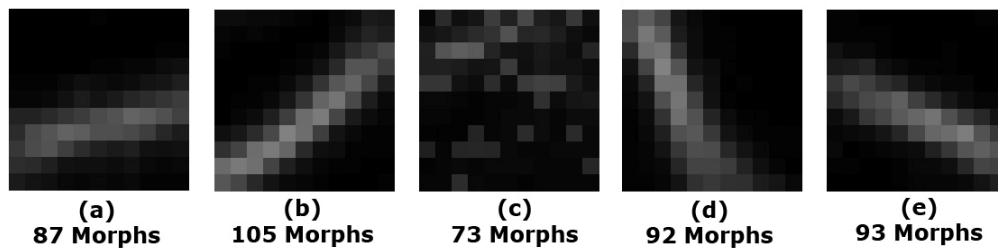

(a)
87 Morphs
(b)
105 Morphs
(c)
73 Morphs
(d)
92 Morphs
(e)
93 Morphs

Fig. 10 After only 450 iterations using a driving function, the feature maps using a driving function are already quite mature, and are unlikely to benefit from further training. Although the figure does not show it, the field maps were nearly at this state with 150 less iterations. Training was done on the image in Fig. 5.
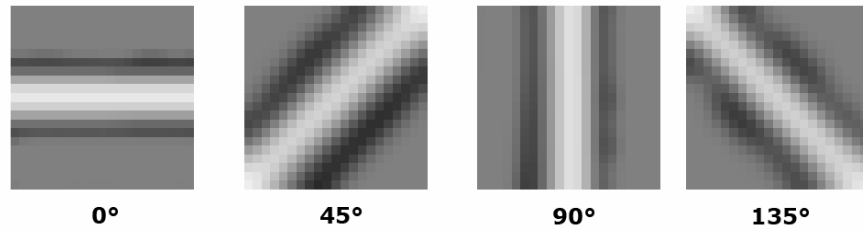
Fig. 11 Artificially generated receptive fields for use in simulation to attempt to learn orientation-selectivity via correlating sensory-invariance to motion of focus point on visual field. Actual orientation-selectivities of fields are labeled under the images. White areas represent areas that are stimulated by light, dark areas are stimulated by darkness, and gray areas are neutral.
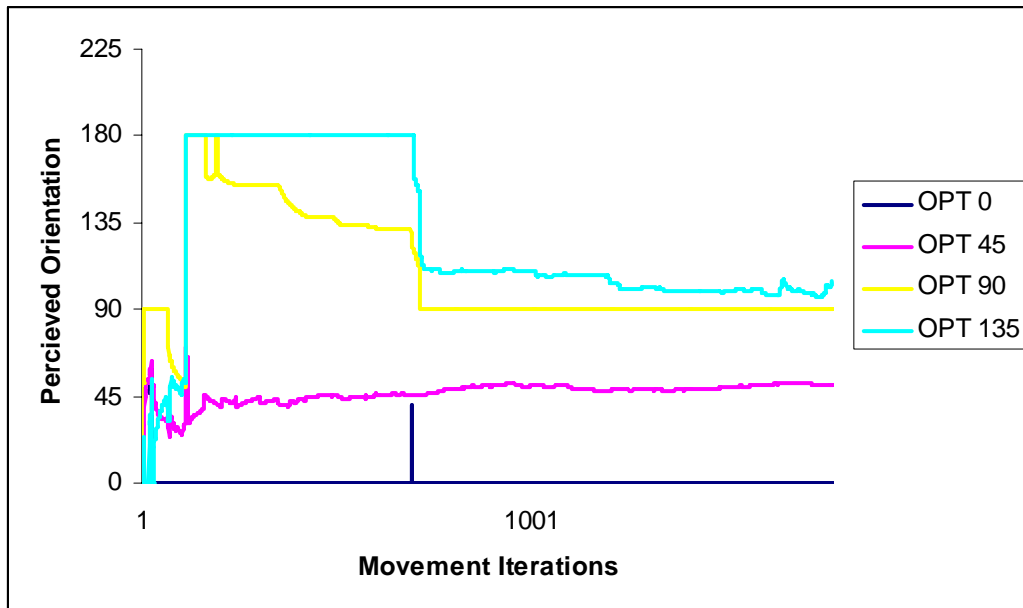

Fig. 12 Learned values of orientation-selectivity of four optimally developed receptive fields, by correlating sensory-invariance with movement over a simple grid visual field (Fig 6, b). The graph shows nearly ideal learning of the receptive fields oriented at 0, 45, and 90 degrees. The learned value for the receptive field representing 135 is perceived to be low. The rapid changes in perceived orientation are due to the threshold k in Eq. 5.
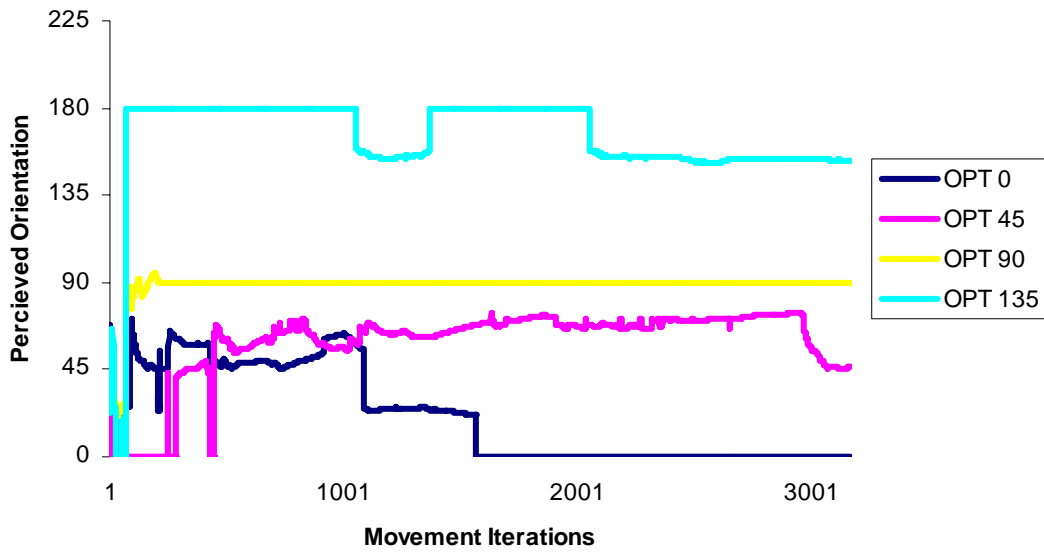
Fig. 13 This graph is similar to Fig. 7, except that this time a grid containing angled lines is used (Fig 6, a). The learned values over time finally approach the correct values, however the perceived value for the 135 degree receptive field is somewhat high, and the edtimate for the 45 degree receptive field takes a long time to correct itself.
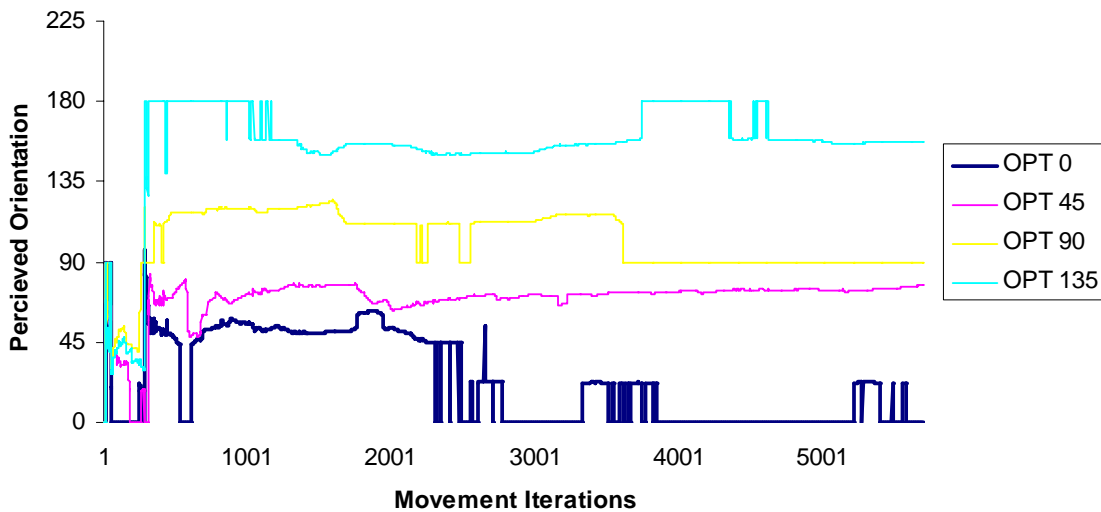

Fig. 14 This graph was generated under the same conditions as the graph in Fig. 8, but the movement path is different. This shows how the effectiveness of the algorithm is dependent on the path traveled and not just correlating sensory-invariance. Additionally, the learned orientations are less accurate than they were in Fig. 8.
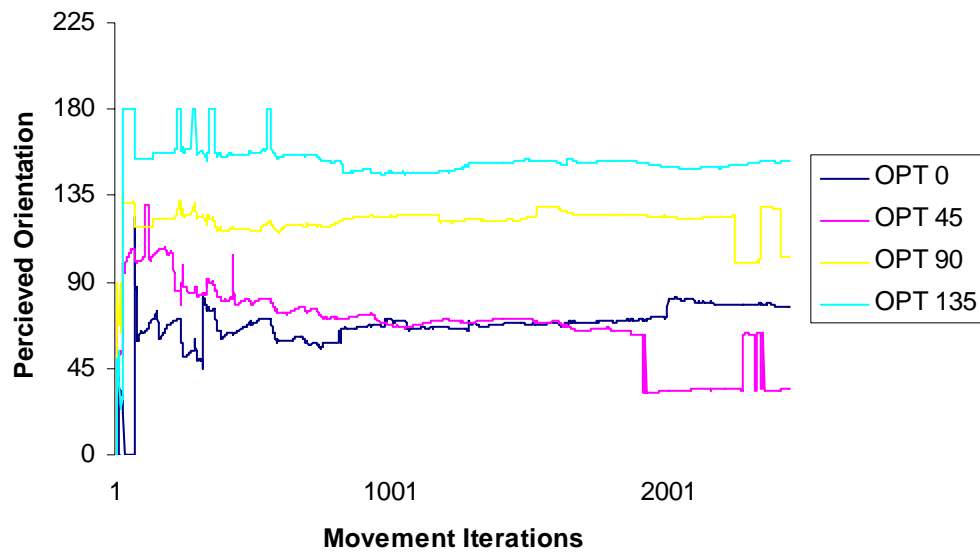
Fig. 15 This graph shows the results of attempting to learn the orientation-selectivity of well-formed neurons by correlating sensory-invariance with focus movement while traversing a real-image visual field (Fig. 5). The orientation of each field is learned to be higher than they actually are except for the 45 degree field. The relative order of orientations is at least learned properly for the majority of the training, until the end when the 0 and 45 degree angles switch.

5. DISCUSSION

In order to evaluate the quality of the receptive field maps that we generated, we consider the following three properties: orientation preference, sparsity, and contrast. By orientation-preference, we mean that the active regions of the field exhibit a line of some specific orientation and translation. By sparsity, we mean that the orientation-preferences among the set of fields are sparsely distributed from 0-360 degrees. Finally, by contrast, we mean that the active regions of the field are clearly distinguished from the inactive regions.

Orientation-preference is important because the purpose of the fields are to match the orientations of lines evident in small samples of larger images, so that an accurate encoding of the image may be formed. Sparsity is important for the same reason, because if the fields all represent similar angles, the encoding of an unmatched angle would be inaccurate. Contrast is not so important for actual implementation of

the feature maps because internal mechanisms could easily increase the "contrast" in a biological system, but rather it is important because high contrast may increase the confidence in the results of a map configuration.

We found that training with smaller receptive fields provided much faster distribution and convergence of the field maps, because the random receptive field initializations had less deviation from the lines of orientation selectivity. For instance, if the receptive fields were 2x2, many random combinations would already be in the form of oriented "lines", but with dimensions of 10x10, the probability of the random points naturally aligning into shapes similar to the visual field is much smaller.

The effect of the randomness was to make the entire set of fields so dissimilar from the visual field samples as to cause the first morphed field to be continuously the best choice until damping of stimulation due to age reduces the stimulation below the level of the noise patterns with heightened stimulation. To overcome this

problem in our tests, we introduced a higher factor on the first exponential, which gave very high initial stimulation for nascent fields. Perhaps a better solution for the future would be to attempt to simulate initial formations due to retinal or PGO waves.

We found that training with our sensory-invariant driving function, using 4-6 receptive fields with 11x11 dimensions, the receptive field maps would all converge to a fairly stable state after about 300 movement iterations (See Fig. 8). Generally, the resultant feature maps would have very good orientation selectivity, high contrast, and high sparsity. One interesting thing to note, however, is that frequently there will be one field which does not exhibit any orientation preference, and instead takes on the form of a vague circular or random noise feature. Even with increased iterations this feature map was not observed to develop to the same level as the other fields. This presence of this field indicates an insufficient number of receptive fields to accurately represent all the features of the image, and it is a combination of all the other commonly sampled features.

After removing the sensory-invariant driver and using random image sampling for each training iteration, the resulting feature maps after an extremely high number of iterations resemble features from the image, but these features are often not oriented lines as desired (see Fig. 7). Additionally, removing the sensory-invariant driver greatly increases the convergence time. For example, it took nearly the full 2000 iterations to form the vague features in Fig. 7, whereas fields exhibiting much greater contrast, sparsity, and orientation-selectivity are developed after only several hundred iterations when the driver function is used (Fig. 10).

Perhaps the most attractive advantage to using the sensory-invariant driver approach is that it allows correlations between movement and action to be made, which can be used to learn

the orientations of receptive feature maps as they are forming.

Since receptive fields are mutable, the brain must learn which orientations are represented by specific fields after the fields have developed. In order to test only the method of perceiving orientation-selectivity of field maps, we started with artificially well-formed receptive fields (see Fig. 11). Although we tested these two properties separately, they would both be in effect at the same time.

To test the theory behind the method of correlating invariance with movement, we first used grid-patterns as visual fields because when the focus is on any grid line, movement parallel to that line should stimulate the same neuron repeatedly. Using a simple square-grid (Fig. 6b), the results were fairly accurate after about 1000 movement iterations. However, the estimates for the angles not represented in the field (45 and 135) were not as accurate as the angles that were represented (0 and 90).

Using a more complicated grid as the visual field that contains lines oriented at 45 and 135 degree angles in addition to 0 and 90 degree angles (Fig. 6a), the results were not visibly improved. This is likely to be due to the intersections of lines, where high sensory-invariance is maintained by moving in any direction. Also, the graphs indicate the path-sensitivity of the results, because while Fig. 13 and Fig. 14 were run under the same conditions, Fig. 13 happened to produce better results simply because of the path (sequence of actions) that was taken.

Finally, we tested on a natural image (Fig. 5)[*]. Although the relative order of the orientations

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[*] The convoluted image shown in Fig. 5b is not exactly what was used here, because unlike the previous experiment where black represented areas of unimportance, gray represents unimportance in this

was learned properly for the majority of the time, this was eventually unlearned after significant iterations, and the estimated values are all significantly high.

While the results shown here are not conclusive enough to show that action and sensory-invariance are critically important, they do suggest the possibility.

Perhaps by attempting to apply the principles of reinforcement learning, action, and sensory-invariance to an even more biologically accurate model, more robust methods may emerge. In our research we represented receptive fields as image maps, where the intensity of each pixel represented the results of thousands or millions of dendritic connections and weights all the way from the retina into V1. While these weights are indeed mutable, it may be that the way in which they mutate make possible different kinds of algorithms for formation of receptive fields in V1 neurons.

For instance, intermediate cells in V1 may form even more primitive receptive field shapes that are used in the learning and composition of orientation-selective receptive fields. Then, changing individual synaptic weights could result in changing the activation levels of patterns and features within a neuron's receptive field, rather than controlling the intensity of individual pixel points in the field. This kind of field could help to explain the apparent presence of Gabor-like patterns in orientation-selective receptive fields, and could be stored and adapted using multilayer neural networks.

6. REFERENCES

[1] Y. Choe and B. Kumar, "Learning the Meaning of Neural Spikes Through Sensory-Invariance Driven Action," Technical Report 2003-8-3, Department of Computer Science, Texas A&M University, 2003.

[2] Y. Choe, and B. Kumar, "Autonomous Acquisition of the Meaning of Sensory States Through Sensory-Invariance Driven Action," Proceedings of the First International Workshop on Biologically Inspired Approaches to Advanced Information Technology (Bio-ADIT 2004), Lausanne, Switzerland, 2004.

[3] J. Jones and L. Palmer, "An Evaluation of the Two-Dimensional Gabor Filter Model of Simple Receptive Fields in Cat Striate Cortex," Journal of Neurophysiology, vol. 58, No. 6, December 1987.

[4] J. Jones and L. Palmer, "The Two-Dimensional Spatial Structure of Simple Receptive Fields in Cat Striate Cortex," Journal of Neurophysiology, vol. 58, No. 6, December 1987.

[5] J. Daugman, "Uncertainty Relation for Resolution in Space, Spatial Frequency, and Orientation Optimized by Two-Dimensional Visual Cortical Filters," J. Opt Soc. Am. A/Vol .2, No. 7 July 1985.

[6] J. Hirsch, "Synaptic Physiology and Receptive Field Structure in the Early Visual Pathway of the Cat," Cerebral Cortex Jan 2003, V 13 N 1.

[7] D. Ringach, "Mapping Receptive Fields in Primary Visual Cortex Area," J. Physiol 558.3 2004, pp 717-728.

[8] N. Rust, O. Schwartz, J. Movshon, and E. Simoncelli, "Spatiotemporal Elements of Macaque V1 Receptive Fields," Neuron, Vol. 46, 945-956, June 16, 2005.

[9] G. Yang and R. Masland, "Receptive Fields and Dendritic Structure of Directionally

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experiment. For this reason, the pixel intensities in Fig. 5b were increased to make the black pixels gray.

Selective Retinal Ganglion Cells," The Journal of Neuroscience, Sep. 1994, 14(9): 5267-5280.

[10] J. Read and B. Cumming, "Measuring V1 Receptive Fields Despite Eye Movements In Awake Monkeys," J. Neurophysiology, Apr. 23, 2003.

[11] G. Granlund, "Does Vision Inevitably Have to be Active?" Computer Vision Laboratory, Linkoping University S-581 83 Linkoping, Sweden.

[12] T. Hesselroth and K. Schulten, "Receptive Field and Feature Map Formation in the Primary Visual Cortex via Hebbian Learning with Inhibitory Feedback," Dept. of Physics and Beckman Institute, University of Illinois, April 29, 2005.

[13] A. Hyvarinen and E. Oja, "Independent Component Analysis: Algorithms and Applications," Neural Networks 13, 2000, pp 411-430.

[14] C. Law and L. Cooper, "Formation of Receptive Fields in Realistic Visual Environments According to the Bienenstock, Cooper, and Munro (BCM) Theory," Proc. Natl. Acad. Sci, Vol. 91, pp. 7797-7801, August 1994.

[15] E. Bienenstock, L. Cooper, P. Munro, "Theory for the Development of Neuron Selectivity: Orientation Specificity and Binocular Interaction in Visual Cortex," The Journal of Neuroscience, Vol.2, No. 1, pp. 32-48, January 1982.

[16] H. Shankar, "Co-Development of Sensory and Motor Repertoire," Dept. of Computer Science, Texas A&M University, 2004.

[17] J. Stone, "Independent Component Analysis: An Introduction," TRENDS in Cognitivie Sciences, Vol. 6 No.2, February 2002.

[18] B. Blais, N. Intrator, H. Shouval and L. Cooper, "Receptive Field Formation in Natural Scene Environments: Comparison of Single Cell Learning Rules," Brown University Physics Department and Institute for Brain and Neural Systems, Feb 23, 1998.

[19] B. Olshausen and D. Field, "Natural Image Statistics and Efficient Coding," Network: Computation in Neural Systems 7 (1996), pp. 333-339.

[20] B. Olshausen and D. Field, "Wavelet-like Receptive Fields Emerge from a Network That Learns Sparse Codes for Natural Images," Dept. of Psychology, Cornell University, April 28, 1996.

[21] E. Simoncelli and B. Olshausen, "Natural Image Statistics and Neural Representation," Annu. Rev. Neuroscience, 2001. 24: pp. 1193-1216.

[22] P. Hancock, V. Bruce and A. Burton, "Testing Principal Component Representations for Faces," Department of Psychology, University of Sterling & University of Glasgow, UK.

[23] O. Packer and D. Dacey, "Receptive Field Structure of H1 Horizontal Cells in Macaque Monkey Retina," Journal of Vision (2002), 2, pp.272-292.

[24] R. Wong, "Retinal Waves and Visual System Development," Annu. Rev. Neuroscience 1999.22: pp. 29-47.

[25] R. Mikkulainen, J. Bednar, Y. Choe, *Computational Maps in the Visual Cortex*. Berlin, Heidelberg, New York, Hong Kong, London, Milan, Paris, Tokyo: Springer, 2004.