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REVIEW ARTICLE

Mathematical Logic Underlying the Receptive Field Organization of Neurons in Mammalian Primary Visual Cortex

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Abstract

With the camera-type eyes which have a specialized function for the image-forming vision, the primary visual cortex (V1) is common to all mammalian species, and is considered to be established at early stage in mammalian evolution, being inherited in all lineages. A defining characteristic of the mammalian V1 is the presence of orientation-selective neurons (or simple cells), which are activated in response to line-, or edge- stimuli in some orientations better than others. It is not yet known as for what were the driving forces that made the robust emergence of such a common design for V1 neurons in mammalian evolution. In this study, I address this problem by employing mathematical approach to arithmetizing various kind of geometries. The formalism which I employ here can not only account for an essential role of the receptive field organization of orientation-selective V1 neurons to the processing of images, but also be used to focus in a concise way to develop mathematical logic as a model of how visual neurons work.

Key words: The primary visual cortex (V1); orientation-selective neurons; image-forming vision; axiomatization of geometry

Introduction

Light in external environment plays a central role in modulating the behavior and physiology of most animals. Then, eye evolution leading to the development of vision together with locomotion/navigation may be an important aspect of the evolution of animals in ecological systems. Nilsson [1] has indicated that essential evolutionary innovations of screening pigment, membrane stacking, focusing optics, and sufficiently large apertures, together with the development of specialized nervous system, enable high-resolution image-forming vision, which has evolved in only vertebrates, cephalopods, and arthropods. The high-resolution image-forming vision allows for the advancement of visually guided behaviors such as object recognition (enabling detection of foods, pursuit of prey, and detection of predator), navigation and visual communication, which are generated by respectively specialized nervous systems.

With the camera-type eyes which have a specialized function for the image-forming vision, the visual cortex is common to all mammalian species: visual inputs are first relayed from the retina through the lateral geniculate nucleus (LGN, the thalamus) to the primary visual cortex (V1, striate cortex) and from there sequentially dispatched to extrastriate cortical areas. The number of visual cortical areas varies across species, but a primary visual cortex (V1) is commonly demonstrated in all mammalian species, and the basic features of V1 are conserved in different species: V1 can be delimited precisely on the basis of the cytoarchitecture (the presence of a granular layer), myelination, the presence of a visuotopic map, known as retinotopy, a well-defined pattern of geniculo-cortical afferents, and distinct properties of neuronal response (the receptive field size and the orientation-selectivity) [2]; V1 versus the extrastriate areas can be demarcated on the basis of their cytochrome oxidase activity in the cells [3,4]. Recently, geniculo-cortical inputs are revealed to drive the genetic distinction between V1 and the extrastriate areas. Chou et al. [5] have shown that the distinct properties and functions of V1 from the higher-order visual areas are largely determined by their distinctively patterned expression of sets of genes: transcription factors (TFs) expressed by progenitors determine the size and position of V1, by specifying respective visual cortical fields differentiating into V1 and the higher-order areas in the occipital cortex. Thus, V1 is considered to be established at early stage in mammalian evolution and inherited in all mammalian lineages. Yang et al. [6] have pointed out that the primate V1 neurons are regulated in a prototypical (or archetypical) manner, which differs significantly from the neuronal signaling mechanisms regulating the neural circuits more recently evolved in the primate dorso-lateral prefrontal cortex (dlPFC). They have shown that V1 neuron firing to visual stimuli depends on α-amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid (AMPA) receptors, with subtle N-methyl-D-aspartate (NMDA) receptor contribution, while dlPFC neuron firing depends primarily on NMDA receptors:

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in V1, adenosine 3',5'-cyclic monophosphate (cAMP) signaling and hyperpolarization-activated cyclic nucleotide-gated (HCN) channel opening strength neuronal firing, and AMPA receptors directly depolarize the postsynaptic neurons, and serve for the activation of the neurons by feed-forward connections, which determine their tuning.

A defining characteristic of mammalian V1 is the presence of orientation-selective (or simple) cells that respond to lines, bars, or edges in some orientations better than others. In some mammals such as primates and carnivores, which have convergent, frontally-oriented eyes granting a high degree of binocular overlap, the orientation-selective neurons are organized into columnar structures [7,8], and in other animals such as rodents, which have laterally-placed eyes resulting in panoramic field with narrow binocular overlap, there is no columnar organization of orientation preference but individual neurons exhibit remarkable orientation-selectivity to line- or edge-stimuli [9,10]. Recent studies suggest that the maps of orientation preference are generated onto the topographical scaffolds provided by geniculo-cortical afferents [11-14]. Vidyasagar and Eysel [12] have pointed out that during development, retinal dendritic fields may provide V1 neurons with the input signals tuned to orientations. Kaschube et al. [15] examined the maps of orientation preference in V1 for three phylogenetically and ecologically diverse species, i.e., the ferret, tree shrew, and galago, and found a common principle for the construction of functional maps: long-range connectivity mediates neural interactions leading to the construction of the orientation preference maps. These facts are consistent with the view of eye evolution that the evolution of the complex 'visual eyes', i.e., image forming, requires the co-evolution of elaborate neural circuits, some of which would eventually become a part of brain such as the visual cortex [1]. Thus, the response selectivity of V1 neurons to the orientation of a line segment in the visual field has been considered to be a hallmark of the primary visual cortex, and the orientation selectivity and/or the line detection have commonly served as a basis in many studies on cortical computations of visual information [9,16]. However, it is not yet known what a functional role the orientation-selective neurons have fundamentally in image-forming vision, and whether this spatial organization is essential or not. The present study addresses this problem.

Fundamental properties of neural architecture in the pathway from retina to V1

What were the driving forces that made the robust emergence of orientation-selective V1 neurons? From the view of evolution (as shown in Figure 1 in [1]), the whole-evolutionary process starts by genetic variation causing variation in structure and function of a certain sensory system, and this results in variation in the behavior that relies on the information provided by the sensory system, then, these variations finally cause the change in fitness on which natural selection acts. Thus, the modifications of sensory system are driven and maintained ultimately depending on whether they satisfy the requirements for improving fitness. From this, it follows that the robust emergence of orientation-selective simple cells in mammalian V1 may be a consequence of the fact that such a neural architecture in V1 has successfully improved fitness, by meeting the requirements for adequate processing of the information, that is, geometry, provided by the camera-type eyes, i.e. image-forming.

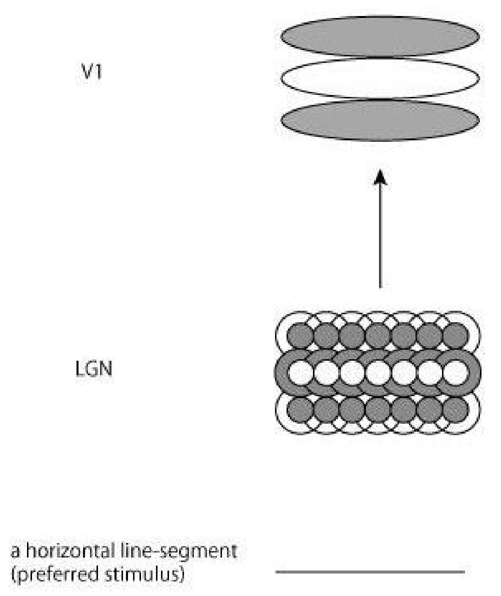

Figure 1 Receptive field organization of a simple cell (top) A simple theoretical model :each simple cell sums inputs from LGN neurons with neighboring/aligned receptive field locations, resulting in an elongated receptive field, which makes the cell most responsive to a line segment of a particular orientation (horizontal in this case) (bottom).

To get whole picture by proceeding mathematically, as a first step, I will review what is commonly accepted concerning the fundamental properties of the receptive field organizations of neurons in the visual pathway up to V1.

Through focusing optics, an image of external world is formed on an array of photoreceptors forming retina. The spatial positions (or topological organization) of individual ganglion cells in the retina are preserved by the spatial organization of the neurons in the lateral geniculate nucleus (LGN) layers in such a way that the back of the nucleus contains neurons whose receptive fields are near fovea, and towards the front of the nucleus, the receptive field locations of neurons become increasingly peripheral. This spatial organization of neurons, called retinotopy, is preserved by the neural signals in V1. Since the receptive fields of retinal neurons and LGN neurons are circular, they respond preferentially to 'points', almost equally well to all stimulus orientations. Orientation selectivity is an emerging receptive- field property of neurons within V1. The receptive field of each simple cell in V1 consists of excitatory and inhibitory sub-areas adjacent to each other, as illustrated in Figure1, and the orientation selectivity has been explained by a simple theoretical model that each simple cell sums inputs from LGN neurons with neighboring/aligned receptive field locations, resulting in an elongated receptive field and making the cell most responsive to a stimulus (line or edge) oriented along the main axis of the receptive field. The simple cells not only respond selectively to elongated bars, or edges, but also perform length summation, i.e., their responses increase with an elongation of the bar length up to some length, for which the response plateaus. Recent studies have revealed that most V1 neurons have the property, called end-stopping, in some degree; their responses increase with an increase in bar length up to some limit, but then as the bar is elongated, the response is inhibited. Pack et al. [17] have shown that the end-stopped V1 neurons begin to respond to a bar or line segment presented within their receptive field, and after 20-30ms they respond to the end points of the bar.

Three points should be noted here to proceed mathematically. First, because both LGN and retinal neurons have circular receptive fields, at this initial stage of visual processing, all the variables occurring range over elements of a set; the elements are referred to as 'points', and the set as the space. Second, because of the spatial layout, called retinotopy, the topological organization of neurons in LGN parallels the topological organization in the retina, and the topological organization of retinal neurons is preserved also by the retinotopically arranged neural signals in V1. Thirdly, neural processes are described in terms of their participant neurons, which are considered to perform various arithmetic operations. Silver [18] has shown that neurons with various morphologies (simple or complex) possess many biophysical mechanisms allowing to perform arithmetic operations on their input-signals: the mechanisms arising from synaptic plasticity, synaptic noise, and somatic and dendritic conductance confer computational power of rational operations (addition, subtraction, multiplication, and division) on individual neurons.

These three points clarify that in the image-forming vision, a successful construction of neural architecture at least in V1 would aim at describing every geometrical fact, given as a fixed number of 'points' in a set of photoreceptor-array, by means of arithmetic. I propose that the concept of the receptive field organization as a logical entity for the arithmetization of geometry is instrumental in advancing our knowledge of the receptive field function in V1 neurons. Thus, the goal of the present quest is exactly to draw out the mathematical logic and make it explicit by employing the mathematical approach to arithmetize the various kind of geometries.

Mathematical formulation

Axiomatization of a geometry in first-order logic, i.e., producing a system of axioms by only using first-order logic, is an approach to enunciate a "simple" and "complete" system of "mutually independent" axioms, from which all the theorems of geometry can be deduced by only using first-order logic [19]. The axioms are formulated for undefined variables such as "points", and they establish geometrical relations that the variables have to satisfy in a geometrical space. The system of the axioms is highly significant in the arithmetization of geometries, because the conception of the axioms reflects an expression of observation of geometrical facts experienced in the space. Thus, by means of the axiomatization, the whole system of geometry can be constructed by purely logical and arithmetic means.

In an elementary version of the axiomatization of geometry, every model of that system of axioms is known to be isomorphic to a certain algebraic structure. Tarski [20] has exhibited that the elementary geometry is formalized within elementary logic, i.e., first-order predicate calculus, with one kind of variables standing for 'points', and two notions of relation, that is, one is the ternary relation β('betweenness' relation), with $\beta(abc)$ denoting the geometrical fact that a point b lie between a and c , and the other is the quaternary relation $\equiv$ ('equidistance' relation), with $ab\equiv cd$ denoting the geometrical fact that a is as distant from b as c is from d. The first-order logic consists of equality, the sentential connectives of conjunction, disjunction, negation, implication, the biconditional, the universal quantifier, and the existential quantifier. In Tarski's system of axioms [20], all the axioms (thirteen axioms for Euclidean geometry) are formulated and described in terms of the two geometrical (non-logical) notions. Making use of Tarski's results for elementary algebra, Schwabhanser [21] showed a proof for completeness of elementary hyperbolic geometry and the existence of a decision method for this theory. In that proof, formulas were built by means of logical operations of the form 'A=B' (equality between points) and 'AB agl CD' (equidistance relation between points), containing only variables for points, by introducing the notion of 'end', i.e., end-calculus which was developed by Hilbert [22]. It should be noted that the introduction and conception of the two relation symbols fundamentally contribute to the conciseness of Tarski's axiomatization of geometry. The 'betweenness' relation represents the affine aspect of geometry and the 'equidistance' relation represents the metric aspect of geometry. Thus, the two non-logical notions have fundamental roles to formulate in a natural and concise way the laws and definitions involved in the development of Euclidean geometry. The systems of axioms surveyed here show that given 'betweenness' and 'equidistance' relations, geometrical facts can be described by means of arithmetic, containing only one sort of variables standing for 'points'.

Mathematical logic underlying the receptive field organization in V1 neurons

In Tarski's formalization of elementary Euclidean geometry [20], which is isomorphic to an algebraic structure, only points are treated as variables. The formalization contains neither variables of higher orders nor symbols to denote geometrical figures (the straight lines, the circles, the segments, the triangles, and more generally the polygons). Nevertheless, one can express in Tarski's system of axioms all the results of Euclidean geometry which are ordinarily formulated by referring to various classes of geometrical figures and certain relations between geometrical figures, such as congruence and similarity. As Tarski [20] has given a full detail, in terms of two predicators which denote ‘betweenness’ and ‘equidistance’ relations among points, all geometrical notions (or facts) are definable: the geometrical fact that a point *z* lies on the straight line through the points *x* and *y* is formalized by the first-order logical statement that either $\beta(x,y,z)$ or $\beta(y,z,x)$ or $\beta(z,x,y)$ holds, i.e., $\beta(x,y,z) \vee \beta(y,z,x) \vee \beta(z,x,y)$; the geometrical fact that two segments with the end points *x,y* and *x’, y’* are congruent is formalized by $xy \equiv x'y'$, and so on (see [20]).

This argument raises the possibility that the organization of the receptive field of the orientation-selective V1 neurons may have a functional role to represent the two predicates or notions of ‘betweenness’ and ‘equidistance’ relations so that an individual orientation-selective neuron can respond optimally to a straight line segment (defined by the ‘betweenness’ relation) and the length tuning and/or the end-stopping property of the neuron can represent distance/metric defined by the ‘equidistance’ relation. Thus, the receptive field organization of the orientation-selective V1 neurons may serve to give non-logical constants, or primitive notions of ‘betweenness’ and ‘equidistance’ relations, by means of which the full edifice of geometry is formalized within first-order logic/arithmetic for retinal images consisting of one sort of variables, i.e., ‘points’.

Euclidean geometry is the geometry that captures the key characteristics of our spatial experiences. Two-dimensional Euclidean geometry is formalized and arithmetized by Tarski’s system of axioms, which consists of thirteen axioms, by only using first-order predicate calculus, and containing only variables of ‘points’ and the two non-logical constants. For an example, one of the axioms is Five-Segment Axiom, shown in Figure 2: this axiom is fundamental in deriving the theorems of the congruence of angles and triangles from the notion of the equidistance relation (see [23]). Tarski’s system of axioms has been proved to be decidable and complete [20], and provides an adequate basis for the whole of Euclidean geometry. Therefore, given non-logical constants of the ‘betweenness’ and equidistance’ relations by the neural processing of the orientation-selective neurons in V1, the neurons in higher-order visual areas can construct the system of axioms, as given by Tarski’s system of axioms. Taking account of the empirical fact that the retinotopic mapping is characterized as a conformal mapping in primates including human [24, 25], the system of axioms developed by Schwabhauser [21] for elementary hyperbolic geometry may comprehend more precisely the strategies taken by the nervous system in the primate V1. Thus, an exact description of all the geometrical facts, as shown by Takahashi and Ejima [24], is possible by means of these kinds of the system of axioms and the arithmetic operations performed by neurons in the visual cortex.

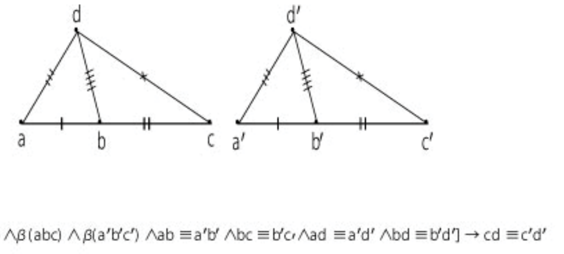

Figure 2 Five-segment Axiom in Tarski’s system of axioms.
The axiom is obtained by using first-order predicate calculus, variables of ‘points’ and two relations of ‘betweenness’ and ‘equidistance’, as shown in the bottom.

Conclusion

The mathematical formalism, which I employ here, can well account for an essential role of the receptive field organization of the orientation-selective V1 neurons to processing of images, i.e., geometry, and hence it can be used to focus in a concise way to develop logic as a model of how visual neurons work. The concept of feature detector has been the driving force behind most researches on vision in neurosciences, biology and computer sciences. By feature detection process, the nervous system is assumed to extract behaviorally/perceptually relevant cues: simple cells in V1 respond selectively to edges, that is, a feature which is more likely to occur in objects in the environment and a relevant cue in object recognition. However, the feature detection hypothesis that individual neurons, or groups of neurons, code for perceptually/behaviorally significant properties of stimuli is doubtful, because a property of the receptive field of neurons and/or activity of individual neurons cannot be directly linked to relevance in a specific behavior. Note that in the image-forming vision, arithmetization of geometry by means of axiomatization is necessary and inevitable for V1 neurons to perform arithmetic operations on their input-signals originated from point sets in an array of photoreceptors in the retina. I suggest that what the nervous system can logically/arithmetically deduce from an image, by means of the construction of the system of axioms, is itself valid in nature, in the sense that geometry deals with the facts manifesting to us in the observation/experience of space, and that the robust emergence of the common receptive field organization of V1 neurons may be a consequence of the fact that it serves for successful construction of the system of axioms to deal with geometry by arithmetic operations performed by individual neurons in the visual cortex.

Ethics: This article does not include research that required ethical approval or permits.

Data Accessibility: No new data were created during the study.

Competing interests: I declare I have no competing interests.

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