Athens Journal of Sciences- Volume 7, Issue 3, September 2020 – Pages 127-142

Could Striate Cortex Microcolumns Serve as the Neural Correlates of Visual Consciousness?

By Walter Alexander Escobar[*] & Megan Slemons[•]

Neural circuit structure studies commonly focus on cell connectivity within circuits and not on the 3-D structure of the circuit itself. In part, this is due to the difficulty of identifying the three-dimensional structure of circuits containing hundreds to thousands of cells. However, given the importance of structure-function relationships in biology, this approach may be missing valuable information related to the properties and activities of these circuits. A case in point being the well-known and studied striate cortex microcolumns found in several mammals. Within the Quantized Visual Awareness (QVA) hypothesis, the specific topology of these microcolumns is thought to be a key factor in determining the type of qualia produced by these neural circuits of the visual cortex. This communication serves as a gentle reminder that we may be overlooking important features of the circuits we study in our rush to understand circuit activity and physiology, especially as it relates to the neural correlates of visual consciousness.

Keywords: *Neural circuits, striate cortex microcolumns, visual awareness, visual consciousness*

Introduction

Researchers have studied neural circuits across many species for decades. The models based on this research take into consideration the various currents (K^+, Na^+, Ca^{++}, etc.) that cross the membranes of neurons and the connectivity of these cells within their respective circuits. In these models, the physical shape of the neural circuit is not considered in the function of the circuit except in rudimentary ways.

As a result, we tend to think of specific circuit topology as noise or irrelevant variations that are not important in terms of the underlying biology. It may be the case that this is indeed true for many neural circuits but we should remain open to the idea that this may not always be true. One of the basic tenets of biology is that structure defines function and it is possible that in certain cases the specific 3-D topology of a circuit is functionally important.

A case in point is the microcolumn circuits we find in the striate cortex (V1) of certain mammals. The cells in this part of the cortex are known to process basic bits of information used for the production of visual experiences. However, the role of V1 in the production of the visual experience itself has remained controversial. Leopold and Logothetis observed that fewer cells in V1 seem to

[*]Senior Lecturer, Department of Biology, Emory University, USA.
[•]Library and IT Services, Center for Digital Scholarship, Woodruff Library, Emory University, USA.

https://doi.org/10.30958/ajs.7-3-1 doi=10.30958/ajs.7-3-1

respond to changes in perception when compared to V4, V5 or the inferior temporal cortex (Leopold and Logothetis 1996, Keliris et al. 2010). The authors interpreted this to indicate a lesser role for V1 in the production of conscious experiences. In other studies, patients with blindsight and a damaged V1 experienced phosphenes when transcranial magnetic stimulation (TMS) was applied to the parietal cortex (Mazzi et al. 2014), indicating that perhaps V1 is not necessary for visual experiences.

In contrast to these studies, the work of many researchers indicates that the recurrent activation of V1 from visual areas like V3, V4, and V5, correlates with the onset of phenomenal visual experiences (Boehler et al. 2008, Cowey and Walsh 2000, Kosslyn et al. 2001, Mehta et al. 2000, Overgaard et al. 2004, Pascual-Leone and Walsh 2001, Silvanto et al. 2005, Tong 2003). This work indicates that the recurrent activation of V1 by the higher centers (V3, V4, V5) is required for the production of visual experiences and when this recurrent activation is inhibited, there is a loss of conscious, visual content. On the whole, the evidence presented here supports the idea that V1 is required for the production of visual experiences.

The Quantized Visual Awareness model (QVA) proposes that V1 microcolumn circuits play a central role in the formation of subjective, visual experiences and it is their specific topology that leads to the production of small, discrete quanta of awareness (qualia) that are integrated into our visual field through temporal synchronization - a phenomenon correlated with conscious perception (Eckhorn et al. 1988, 1993, Eckhorn 1994, Fries et al. 1997, Kreiter and Singer 1996, Singer 1998). These quanta of awareness arise directly from the activation of microcolumns with the type of quale being determined by the specific topology of the microcolumn. Thus, the microcircuit topology is central to understanding what type of quale will be produced (Escobar 2013, 2016).

Fine Structure of the Striate Cortex (V1)

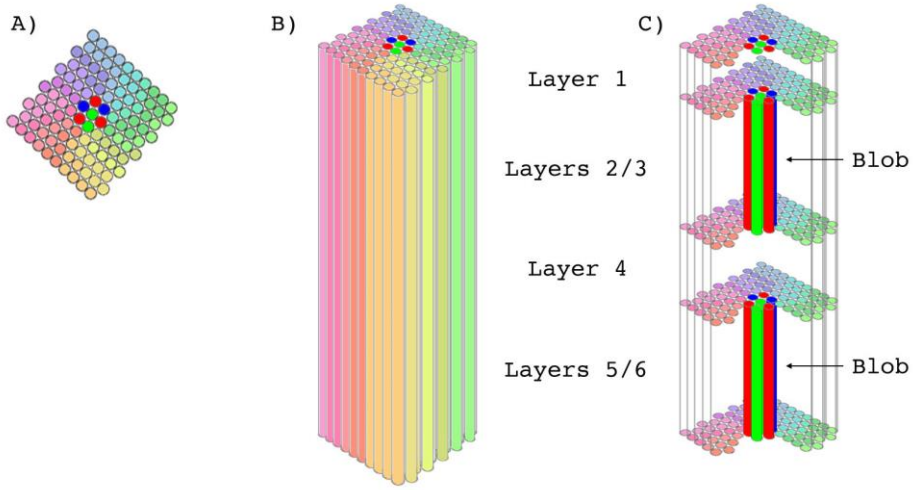
The striate cortex contains ocular dominance columns (ODCs) that correspond to specific points of the visual field (Hubel and Wiesel 1974, Hubel et al. 1978). All of the neural cells and circuits within a specific ODC are tuned to the same eccentricity and polar angle of the visual field and have the same ocular bias. We can think of each ODC as an organizing center used to process various attributes for a given point of the visual field. Within any given ODC there are 50-80 microcolumns (Mountcastle 2003, Peters and Sethares 1991) with diameters in the range of 30 micrometers (Figure 1). Each microcolumn is defined by the bundles of pyramidal cell apical dendrites placed through the center of each column (Peters and Walsh 1972). This anatomy suggests that these microcolumns may act as independent units and this is supported by the fact that there are inhibitory interneurons that line the edges of these columns and create what is known as an inhibitory fringe (Von Bonin and Mehler 1971). Thus, the activation of any given microcolumn inhibits nearby columns.

Early studies by Hubel and Wiesel seemed to indicate that microcolumns are tuned to different stimuli (Hubel and Wiesel 1974). Hubel and Wiesel saw

changes in tuning specificity in distances as small as 30 micrometers, possibly indicating that there was a change in tuning specificity as their electrode moved from one microcolumn to another. QVA predicts that microcolumns are tuned to various visual attributes like color and line orientation. Moreover, these microcolumns contain within their structure the information required to generate a bit of experience or a quale. This experience, by necessity, is very simple like sensing a bit of the color red at a certain point of your visual field. However, given that you have 50-80 microcolumns within each ODC, these simple qualia can be combined into more complex experiences by activating different sets of microcolumns within each ODC.

For the purpose of illustrating this concept, let us imagine that there are a few microcolumn topologies that correspond to color qualia. These might be red, blue, and green. These colored qualia can be combined in the classical sense to create new colors. For example, red and green can be combined to create the sensation of the color yellow in the same way that red and green lights combine additively to form the color yellow. To create the sensation of a vertical yellow line at a specific point in your visual field, you would activate microcolumns tuned to the vertical line orientation as well as red and green colors. In this fashion, it should be possible to generate the sensation of a large number of varied experiences by changing the combination and number of microcolumns contributing to the experience for each point of the visual field. One of the essential principles of QVA is that it allows for a tremendous amount of complexity to arise from the combination of otherwise simple subunits.

Figure 1. *A) Top of an Ocular Dominance Column (ODC). The Circles are the Tops of the Microcolumns contained within an ODC as shown in B). The Various Hues Correspond to Orientation Tuning Covering a Complete set of 180 Degrees. The Red, Blue and Green Microcolumns are used to Process Color. C) These Columns Pass through Blobs – Tissue that stains for Cytochrome Oxidase Activity and is tuned to Color Stimuli*



Source: Adapted from Escobar 2016.

Control over the activity of individual microcolumns is provided by the higher visual centers: V3, V4, and V5. Although there will be activity in V1 microcolumns produced by the incoming data from the eyes, this is not sufficient to induce a phenomenal experience. It is only by reaching gamma synchrony that these columns contribute to phenomenal consciousness (this is described in the Discussion section). Decisions made by V3, V4, and V5 will push the already active V1 microcolumns into gamma synchrony. Given that we are only shifting the activity of V1 microcolumns, these changes in activity may appear small when probed by electrophysiological techniques. Several studies looking at changes of neural activity as a function of changes in perception indicate that fluctuations in V1 activity are of a smaller scale than those seen for higher centers like V4 (Leopold and Logothetis 1996, Keliris et al. 2010).

Consider the phenomenon of color constancy. This occurs when parts of the visual scene are in shadow and the colors of objects within the shadow are made to appear lighter by our own visual system. This occurs so that we may see these objects as having the same color in diverse lighting conditions. Although the specific mechanism by which color constancy arises is not fully understood, this phenomenon must take place in V4 (Witzel and Gegenfurtner 2018). Information arriving at V1 from the eyes is retinotopic in nature (reflecting individual points of the visual field). It is impossible for the required comparisons in lighting to be made at this point in the feedforward sweep (forward movement of information through the visual system). It is only when this information arrives at V4 that distant points of the visual scene can be compared and illumination ratios determined for the scene.

Primed with this information, V4 determines which microcolumns of V1 should be pushed into gamma synchrony. Using the example of the yellow, vertical line above, V4 pushes microcolumns corresponding to red, green and vertical qualia into gamma synchrony while simultaneously activating triplets of red, blue and green qualia (equivalent to white) to lighten the color. Based on this example, we can see the higher visual centers (V3, V4, and V5) are playing a pivotal role in orchestrating the activity of V1 microcolumns and thereby determining which qualia are included in phenomenal consciousness. In most cases, however, these higher visual centers are not the physical location of the neural correlates of visual consciousness.

I have limited my discussion of qualia to just color and line orientation information, but for this hypothesis to be robust, there must be qualia that correspond to the sensations of depth, motion and other aspects of visual experience. QVA proposes that all of these visual properties are produced in the same fashion as that described above and therefore there must be unique microcircuit topologies that correspond to each of these properties.

Although there are millions of microcolumns in V1, QVA predicts there should be a limited set (50-100) of microcircuit topologies (with corresponding simple qualia), which can be combined into a large number of possible visual scenes. Thus, we would expect the same topologies to repeat throughout V1, with the same microcircuit topologies found in many ODCs. Also, these same microcolumn topologies would not be expected in other parts of the occipital

cortex (ex. V2, V3, V4, V5). Currently, there is no other model (cognitive or otherwise) that proposes there should be any repeating microcircuit topologies in the cortex. If this model holds true, it should be possible to look for these same circuit topologies in other animal models since it is likely some of the same microcircuit topologies are used throughout the animal kingdom. For the first time, we may be able to gain quantitative information about subjective experience in humans and animals.

QVA is rooted in the neuroanatomy of the striate cortex, relates well with studies investigating the onset of visual phenomenal experiences, and follows the fundamental principle of all biological systems – all complex biological systems are formed from the many subunits contributing to that system (a principle lacking from many current ideas about consciousness and subjective experience). In addition, this model provides bridging laws that explain how the activation of neural microcircuits is integrated and result in the production of our overall visual consciousness (Block 1996, Lamme 2003).

In an attempt to prime the search for circuits of V1 with repeating topologies we initiated a study of the structure of the striate cortex using images from the Human Brain Project (please see below for a description). These images provide an in-depth look at this tissue, though only in 2 dimensions. It is hoped that studies like these will inspire others to look at this same region with techniques that can probe the structure of these circuits in greater detail.

Materials and Methods

We are using MINC files generated by the Human Brain Project (Amunts et al. 2013). These images can be accessed on the Human Brain Project website (https://www.humanbrainproject.eu/en/) - the resolution of the images is 20 microns per pixel. For this study, we received files of 10 micron resolution from Dr. Allan Evans and Claude Lepage in the Department of Neurology and Neurosurgery, Psychiatry and Biomedical Engineering, McGill University in Montreal, Canada.

Preparing the Original Files for Analysis

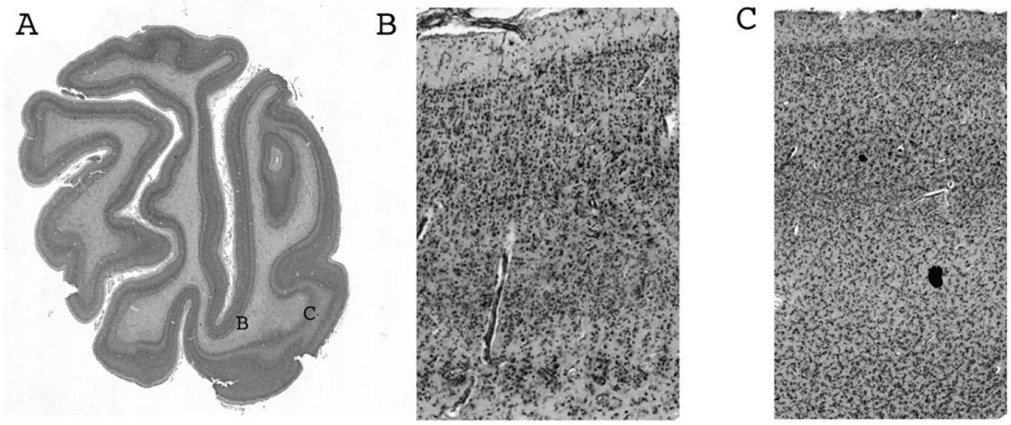
The original brain scan images were stored as MINC (Medical Imaging NetCDF, file extension of .mnc) files - a medical image file format not readable by common image viewing and editing software such as Photoshop or Windows Photo Viewer. To convert these files into a usable format, we used two pieces of medical image software from the National Institutes of Health. We first used MIPAV (Medical Image Processing, Analysis, and Visualization) to convert the MINC files into TIFs, which were still unreadable in Photoshop due to an "unsupported bit depth". The files were then opened in ImageJ and saved as 16-bit TIFs, resulting in files that were readable in Photoshop. (Thank you to Michael Page for assistance with bit-depth troubleshooting.) The images were then cropped in Photoshop to the same extent showing just the relevant area of study on the

scans. Each image was marked with a common origin point from which to measure the distance of each observation. These images were annotated in Photoshop with each observation recorded as a single point with an ID number next to it. Further details on each observation were recorded in a separate spreadsheet.

Results

In the cross sections shown of V1 and V2, it is apparent that there are large differences in the structure of local circuits within these regions (Figure 2). The cell clusters of V1 appear to be distinct and unique in their appearance while the corresponding cells of V2 are not and indeed look more like they are distributed in a random way. This is despite the fact that both V1 and V2 are known to contain complete retinotopic maps and cells of these centers only process local information for specific points of the visual field. Clearly the observed microcolumn structure of V1 is a distinguishing feature and must be important for the function of the striate cortex (V1).

Figure 2. *A) Human Left Hemisphere: Section 300 of The Big Brain Project (Amunts et al. 2013). Tissue was Nissl stained and then digitized (1.0-by-1.0 μm pixel size). This Slice through the Occipital Lobe Includes a Cross Section of V1 and V2. B) The Location of This Image is shown for Reference in A) and is found at the Bottom of the Calcarine Sulcus. Cortical Layer I is at the Top and Layer VI is at the Bottom of this Image. This Image is Representative of V1 Cell Distributions - Clusters of Cells (Especially in Layers V and VI) seem to Aggregate into Distinct Units. C) Please see A) for Location. This Image is Characteristic of Cell Distributions in V2. Notice the Lack of Cell Clusters and Lack of Cell Columns running from the Top (layer I) to Bottom (layer VI) as seen for V1. Brain Image Files were supplied by Alan Evans and Claude Lepage (McGill University) and the DSA MultiSlide Viewer used to Display These Images was developed by David Gutman (Emory University)*



We were limited in our ability to see complete three-dimensional circuit structures since we were required to use two-dimensional (albeit detailed) images

of the brain. In addition, the Nissl stain only allows us to observe cell bodies in the images we use. Given these limitations, our first attempts to identify conserved or repeating circuit structures are confined to looking at cell clustering patterns in layers V and VI of the calcarine sulcus. It is hoped that the large amount of data will allow us to identify repeating cell clustering-patterns in this data and thus describe, in a cursory way, repeating circuit structures.

As observed in Figure 3, the cortical tissue lining the calcarine sulcus can be easily seen in these slices. By visually surveying cell clustering in layers V and VI we have found several cell-clustering patterns that do repeat in various slices (Figure 4). In identifying these patterns, we considered that they would not necessarily have the same orientation and could be rotated by as much as 180 degrees around their vertical or horizontal axis. Unfortunately, this variation in orientation increases the difficulty of identifying these patterns through pattern recognition software. Although we have just begun our studies, we have already identified several patterns as shown in Table 1 along with observed instances of these patterns in the slices available.

Figure 3. *A) Human Left Hemisphere: Section 301 of the Big Brain Project (Amunts et al. 2013). Tissue was Nissl stained and then digitized (10.0-by-10.0 μm Pixel Size). We Began our Survey of the Slices at the Arrow as indicated in the Image and scanned for Cell-Clustering Patterns*

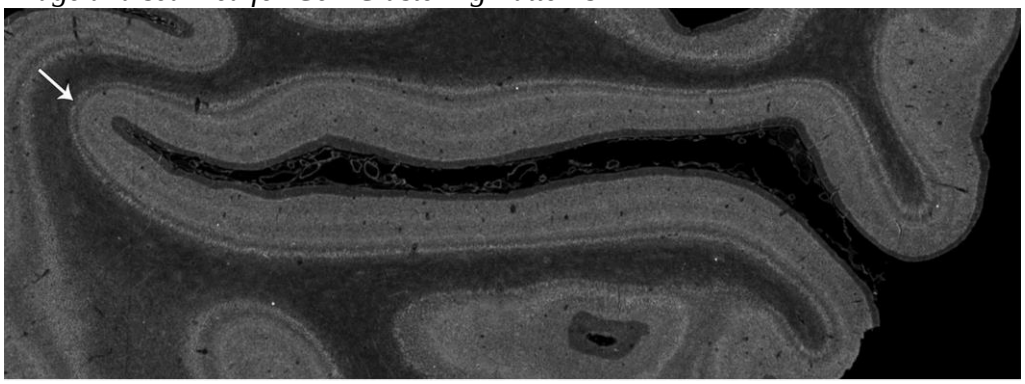


Figure 4. *A) Human Left Hemisphere: Section 301 of the Big Brain Project (Amunts et al. 2013). Tissue was Nissl stained and then digitized (10.0-by-10.0 μm Pixel Size). Clustering Patterns can be More Easily seen in this Magnified Image of Figure 3. Notice the Unique and Clearly Visible Cell Clustering Patterns found in Layers 5 and 6*

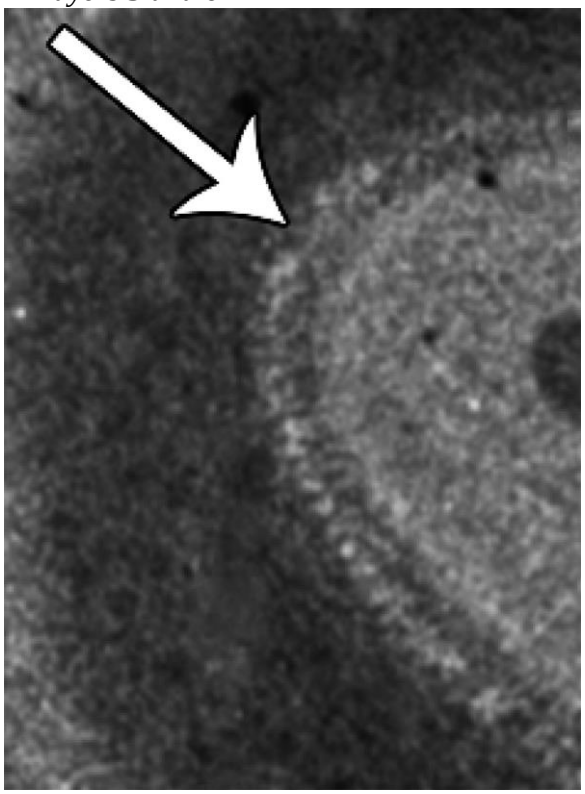


Table 1. *Microcircuit Cell-Clustering Patterns are labelled CP (Clustering Pattern) and numbered in the order that they were identified. Several Instances are shown for Each Type and the Slice of Origin is indicated over the Image of the Cell Clustering Pattern. Some of these Clustering Patterns Resemble Letter Shapes and we have given them Secondary Labels based on this Resemblance*

Label -Primary - Secondary	CP1 "Lamedh"	CP2 "h"	CP3 "YY"	CP4 "ʒ"	CP5 "ω"	CP6 "κ"
Slice #	298 	300 	298 	300 	298 	298 
Slice #	300 	300 	299 	300 	299 	301 
Slice #	300 	300 	300 	300 	300 	
Slice #		300 	301 			

It is understood that these clustering patterns could be parts of larger patterns that are yet to be discovered with a more robust analytical tool. Given that what we see are two-dimensional representations of three-dimensional patterns, it is also possible that some of the discrete patterns we observe could actually be part one larger circuit topology in three-dimensions. For the purposes of initiating this study, we are considering them as unique patterns for the time and until determined otherwise.

We plan to continue cataloging cell-clustering patterns that repeat and hope to have a more complete set in the near future. Our hope is to establish a set of cell clustering-patterns that could be used to train a pattern recognition system to identify them and look at larger swaths of V1.

Discussion

A great degree of structure is easily observed when looking at microcolumns, specifically in layers V and VI of the striate cortex (Figure 4). Many have taken this structure to be of little importance since they believe the activity of these microcircuits only becomes significant at the level of larger populations of cells. Current attempts to understand the functional significance of the neural activity of the striate cortex use a statistical approach by populating large, in-silico circuits with specific cells types (amacrine, chandelier, etc.). The types and numbers of cells are based on known frequencies of these cells in the tissues of interest. Clearly, this approach completely disregards the true and natural structure of these circuits and treats this structure as immaterial (Muralidhar et al. 2014).

Giulio Tononi's Integrated Information Theory (IIT) gives no value to the structure of these cortical columns and completely bypasses the key biological principle that structure defines function. IIT frames information in a more abstract fashion that correlates with the information states of those parts of the brain contributing to consciousness and not with the specific structure of the brain or specific neural circuits of the brain (Tononi 2008, Tononi and Koch 2008). This theory is potent in that it leads to a belief that certain computer systems can be made aware based on their ability to process information dynamically through self-modulation. There is currently much momentum, funding and research based on these ideas. However, as a biologist, I believe this abstraction of the concept of information found in natural systems has completely left the realm of the true nature of the neural correlates of consciousness. It is true that biological systems do possess and store information, but without exception, in nature, this information takes the form of a definite biological structure or electrochemical gradients.

I have postulated the distinct microcolumn 3-D structures of V1 are significant for the production of individual quale and may be key to understanding how visual phenomenal experiences arise. The QVA hypothesis predicts that quanta of awareness (qualia) are incorporated into visual consciousness through the synchronous spiking of microcolumns. Thus, a microcolumn of a certain topology will reproducibly generate simple forms of awareness like the color red when it becomes active (Escobar 2013, 2016). By controlling which microcolumns

within an ocular dominance column become temporally synchronous, the higher centers (V3, V4, V5) can assign specific values for color, depth, orientation, and movement to individual points of the visual field.

The idea that the neural correlates of consciousness could be found in single columns of cells is not new. Francis Crick proposed that the smallest units of consciousness (a node) could be contained within a cortical column of cells (Crick and Koch 2003). In addition, Semir Zeki has suggested for years that there might be "microconsciousnesses" contained within neural networks of the visual cortex and that these "microconsciousnesses" are integrated to form our overall visual experience (Zeki and Bartels 1999, Yu and Zeki 2014, Zeki, 2015a, b).

The Hard Problem

Although we have focused solely on the structure of microcircuits, these microcircuits themselves are not the physical surrogate of qualia. QVA proposes the specifically shaped electromagnetic (EM) fields arising from active microcolumns are the physical aspect of qualia (Escobar 2013, 2016). This proposal is presented within the context of several others who have previously suggested EM fields serve as the surrogate of conscious experience (Pockett et al. 2009, John 2002, McFadden, 2002a, b, 2013). The topology of these small electromagnetic fields determines the unique type of quale that is produced. Moreover, given that these small fields arise in close proximity to each other, we can easily understand how these individual qualia integrate themselves into our larger visual experience. It is well known that nearby electric fields automatically integrate themselves into one larger field. Thus, individual qualia EM fields combine into one larger EM field that contains our visual subjective experience and more.

Electromagnetic fields are wave mechanical phenomena. Wave mechanical processes interfere with each other in what is known as constructive or destructive interference. This is illustrated when water wave troughs come together with wave crests and cancel each other out to create a relatively flat surface. This is an example of destructive interference. Two wave crests coming together to create an even larger crest is an example of constructive interference.

In most material objects, the electromagnetic fields of atoms and molecules interfere with each other in a random manner and this has the general effect of reducing the amplitude (destructive interference) of the integrated fields. This is why inanimate objects don't generally produce large electric or magnetic fields at the macroscopic level. In other words, you do not get a shock when you touch everyday objects or have iron containing materials tugged at by magnetic fields arising from the objects around you.

QVA postulates that the function of V1 microcolumns is to specifically shape EM fields through the constructive and destructive interference arising from various parts of the microcolumn. These specifically shaped microcolumn EM fields correspond to simple forms of awareness (like a point of the color red) that can serve as units for natural selection.

However, all of this does not answer the hard problem: Why are physical processes ever accompanied by experience (Chalmers 1995)? The answer to this comes from understanding that biological systems never create physical properties but use what is already present in nature to enhance reproductive success. For example, mammalian organisms did not invent diffusion but they use it to distribute molecular oxygen throughout their bodies. Organisms did not invent chemical reactions but they use them for their daily metabolism. Electromagnetism was part of nature long before biological systems came into existence and yet many organisms (ex. electric eels) have evolved to use electric or magnetic phenomena to enhance their survivability.

If it is the case that biological systems do not invent universal physical properties, we can reasonably ask, "could some fundamental form of awareness already exist in nature?" In such a case, we would say that biological systems have evolved to utilize this fundamental form of subtle-awareness in nature to produce simple but specific types of awareness in our brains. This is at the heart of understanding why the topology of V1 microcolumns might be so important and why we should focus our attention on their structure. The shape of the microcolumn generates a uniquely shaped EM field. QVA predicts that V1 microcircuits sculpt this natural form of subtle-awareness found in EM fields into discrete and unique instances of simple awareness known as qualia.

What is the Role of Temporal Synchrony in Producing Visual Awareness?

Temporal synchrony plays a dual role. The half-life of any given quale EM field is short. To effectively contribute to the visual experience, it is necessary to continually reactivate a microcircuit to refresh the electromagnetic field it produces. Moreover, by stimulating the appropriate microcircuits in synchrony, we are binding all the respective qualia into one coherent visual image in the same way the refresh rate of a computer screen restimulates pixels to create long-lasting images on your computer displays.

The thalamus is known to be highly connected throughout the cortex and is thought to play a central role in the production of consciousness. Moreover, support for the importance of the thalamus in consciousness is suggested by work using anesthetics with their targeted effect on the thalamus and the resultant loss of consciousness. Unlike some current theories that focus on the thalamus as the source of consciousness, QVA postulates the importance of the thalamus is based on its role of supporting temporal synchrony within the cortex.

The part of the thalamus that connects directly to V1 is the lateral geniculate nucleus (LGN). This connection serves as the dominant road by which visual information reaches the visual cortex. Moreover, thalomocortical circuits that connect the thalamus and V1 are well known to have a pacemaker like quality (Llinás and Ribary 2001). The reticular formation of the thalamus sends subthreshold EPSPs to V1 microcircuits and it is believed that reentrant communication from the higher visual centers (ex. V3, V4, V5) pushes these microcircuits past their threshold and initiates gamma synchrony for selected microcircuits (Escobar 2016). Thus, the thalamus has a pivotal role in establishing

temporal synchrony and is directly contributing to the process of binding individual qualia into our overall visual experience. Without this rhythmic, thalamic, subthreshold-priming (ex. in response to the application of anesthetics), the cerebral cortex continues to exhibit some neural activity but this activity cannot be bound into a coherent, conscious experience and the individual would appear, for all intents and purposes, unconscious.

Conclusions

QVA postulates that, at least, the V1 microcolumns of several primates (macaques and humans for example), shape a fundamental form of awareness in electromagnetic fields through constructive and destructive interference.* This is highly dependent on the topology of the microcircuit itself and so the shape of the microcircuit will yield specific but simple forms of awareness like a point of red, green or blue.

The electromagnetic nature of these fields allows them to integrate themselves instantaneously into a larger field that contains other visual qualia. Together, these bits of awareness (arising from the millions of microcolumns in V1) produce our visual field.

The half-life of any given quale EM field is exceedingly short. Thus, a microcolumn can only significantly contribute to a visual experience through temporal synchrony since this allows each quale contribution to persist in the overall brain EM field. In addition, by producing these bits of awareness in a synchronous manner, we bind the individual qualia into a coherent experience in a manner similar to the refresh rate of a computer display.

Predictions that arise from this hypothesis are that we would expect repeating microcircuit structures since the same types of qualia would be found in a large proportion of the ocular dominance columns distributed throughout V1. Although there are millions of microcolumns in V1, there may only be 50-100 types since we can combine them to create an infinite number of possible visual representations. Currently, there is no cognitive or subjective experience theory that predicts repeating microcircuit structures in V1 of the occipital cortex.

ODCs correspond to individual points of the visual field and serve the purpose of being organizing centers for the 50-80 microcolumns they contain. This system would confer exquisite control of visual experiences to the visual cortex since any number of possible combinations of quale could be specified for each point of the visual field. Please review the example yellow vertical line described above.

In addition, to the predictions listed above, QVA also proposes that conserved (repeating) circuit structures should not be distributed randomly in V1. Distribution patterns should resemble the observed orientation-tuning pin wheel patterns (Crair et al. 1997) and location of blobs (Bartfeld and Grinvald 1992) observed in V1. A match between microcolumn-topology distribution patterns and these other listed patterns would support QVA since no such match is predicted by any other theory or model.

We have begun a rudimentary study of the structure of striate cortex in layers V and VI. The tools we have available at this time are simple but, through our simple approach, we have identified repeating clustering patterns in our target tissue. We realize this does not prove the QVA hypothesis but is only consistent with QVA. To truly establish QVA as a model that accurately describes the production of visual awareness it will be necessary to probe the structure of this region of the cortex with techniques that offer greater precision. We are hopeful that in the coming years the ability to describe the topology of neural circuits containing hundreds of neurons will become a common technology that can be used to answer some of the questions we raise here.

Notes

*A question can be raised about natural EM fields and their effect on the EM fields created by the brain. Transcranial magnetic stimulation (TMS) studies clearly show that brain EM fields can be disrupted by an external field with corresponding effects on conscious perception (Cowey and Walsh 2000, Overgaardet al. 2004). However, it is also clear that TMS generates fields with a much greater local amplitude than say the geomagnetic field of our planet. It is likely the cranium offers enough insulation to prevent significant alteration of brain EM fields since we do not normally experience the disruptions to conscious perception (the perception of phosphenes for example) that routinely occur when the visual cortex is stimulated with TMS.

Aknowledgements

Part of the work in identifying cell cluster topologies was accomplished through the help of undergraduate students in the course Biology 410 (Perception and the Neural Correlates of Consciousness). Below is a list of the names of participating students listed alphabetically by last name: Sudeep Aditham, Evan Altschuler, Talah Bakdash, Triston Charlson, John Delgado, Ronnie Festok, Megan Jiang, Jordan Peyrot Des Gachons, Aditya Prakash, Priyadharshini Rathakrishnan, Sarah Romanelli, Jae Shim, Rishi Varan, Zhuoyang Ye, Teresa Zheng.

References

Amunts K, Lepage C, Borgeat L, Mohlberg H, Dickscheid T, Rousseau MÉ et al. (2013) BigBrain: an ultrahigh-resolution 3D human brain model. *Science* 340(6139): 1472–1475.

Bartfeld E, Grinvald A (1992) Relationships between orientation-preference pinwheels, cytochrome oxidase blobs, and ocular-dominance columns in primate striate cortex. *Proceedings of the National Academy of Sciences USA* 89(24): 11905–11909.

Block N (1996) How can we find the neural correlate of consciousness? *Trends in Neurosciences* 19(11): 456–459.

Boehler C, Schoenfeld M, Heinze HJ, Hopf JM (2008) Rapid recurrent processing gates awareness in primary cortex. *Proceedings of the National Academy of Sciences* 105(25): 8742–8747.

Chalmers DJ (1995) Facing up to the problem of consciousness. *Journal of Consciousness Studies* 2(Jan): 200–219.

Cowey A, Walsh V (2000) Magnetically induced phosphenes in sighted, blind and blindsighted observers. *Neuroreport* 11(14): 3269–3273.

Crair MC, Ruthazer E, Gillespie D, Stryker M (1997) Ocular dominance peaks at pinwheel center singularities of the orientation map in cat visual cortex. *Journal of Neurophysiology* 77(6): 3381–3385.

Crick F, Koch C (2003) A Framework for Consciousness. *Nature Neuroscience* 6(2): 119–126.

Eckhorn R, Bauer R, Jordan W, Brosch M, Kruse W, Munk M et al. (1988) Coherent oscillations: a mechanism of feature linking in the visual cortex? Multiple electrode and correlation analyses in the cat. *Biological Cybernetics* 60(2): 121–130.

Eckhorn R, Frien A, Bauer R, Woelbern T, Kehr H (1993) High frequency (60-90 Hz) oscillations in primary visual cortex of awake monkey. *Neuroreport* 4(3): 243–246.

Eckhorn R (1994) Oscillatory and non-oscillatory synchronizations in the visual cortex and their possible roles in associations of visual features. *Progress in Brain Research* 102(Mar): 405–426.

Escobar WA (2013) Quantized Visual Awareness. *Frontiers in Psychology* 4(Nov): 1–11.

Escobar A (2016) QVA: A massively parallel model for vision. *Psychology of Consciousness: Theory, Research, and Practice* 3(3): 222–238.

Fries P, Roelfsema PR, Engel AK, König P, Singer W (1997) Synchronization of oscillatory responses in visual cortex correlates with perception in interocular rivalry. *Proceedings of the National Academy of Sciences USA* 94(23): 12699–12704.

Hubel D, Wiesel T (1974) Sequence Regularity and Geometry of Orientation Columns in the Monkey Striate Cortex. *Journal of Comparative Neurology* 158(3): 267–294.

Hubel D, Wiesel TN, Stryker M (1978) Anatomical demonstration of orientation columns in macaque monkey. *The Journal of Comparative Neurology* 177(3): 361–379.

John E (2002) The neurophysics of consciousness. *Brain Research Reviews* 39(1): 1–28.

Keliris GA, Logothetis NK, Tolias AS (2010) The role of the primary visual cortex in perceptual suppression of salient visual stimuli. *The Journal of Neuroscience* 30(37): 12353–12365.

Kosslyn SM, Ganis G, Thompson WL (2001) Neural Foundations of Imagery. *Nature Reviews | Neuroscience* 2(9): 635–642.

Kreiter AK, Singer W (1996) Stimulus-dependent synchronization of neuronal responses in the visual cortex of the awake macaque monkey. *The Journal of Neuroscience* 16(7): 2381–2396.

Lamme VA (2003) Why visual attention and awareness are different. *Trends in Cobnitive Sciences* 7(1): 12–18.

Leopold D, Logothetis N (1996) Activity-changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature* 379(Feb): 549–553.

Llinás R, Ribary U (2001) Consciousness and the brain: the thalamocortical dialogue in health and disease. *Annals of the New York Academy of Sciences* 929(Apr): 166–175.

Mazzi C, Mancini F, Savazzi S (2014) Can IPS reach visual awareness without V1? Evidence from TMS in healthy subjects and hemianopic patients. *Neurophysiologia* 64(Nov): 134–144.

McFadden J (2002a) Synchronous firing and its influence on the brain's electromagnetic field. *Journal of Consciousness Studies* 9(4): 23–50.

McFadden J (2002b) The conscious electromagnetic information (cemi) field theory: the hard problem made easy? *Journal of Consciousness Studies* 9(8): 45–60.
McFadden J (2013) CEMI field theory: closing the loop. *Journal of Consciousness Studies* 20(1-2): 153–168.
Mehta AU (2000) Intermodal selective attention in monkeys I: distribution and timing across visual areas. *Cerebral Cortex* 10(4): 343–358.
Mountcastle V (2003) Introduction. *Cerebral Cortex* 13(1): 2–4.
Muralidhar S, Wang Y, Markram H (2014) Synaptic and cellular organization of layer 1 of the developing rat somatosensory cortex. *Frontiers in Neuroanatomy* 7(Article 52): 1–17
Overgaard M, Nielsen J, Fuglsang-Fredricksen A (2004) A TMS study of the ventral projections from V1 with implications for the finding of neural correlates of consciousness. *Brain and Cognition* 54(1): 58–64.
Pascual-Leone A, Walsh V (2001) Fast backprojections from the motion to the primary visual area necessary for visual awareness. *Science* 292(5516): 510–512.
Peters A, Sethares C (1991) Organization of pyramidal neurons in area 17 of monkey visual cortex. *The Journal of Comparative Neurobiology* 306(1): 1–23.
Peters A, Walsh M (1972) A Study of the organization of apical dendrites in the somatic sensory cortex of the rat. *Journal of Comparative Neurology* 144(3): 253–268.
Pockett S, Bold GEJ, Freeman WJ (2009) EEG synchrony during a perceptual-cognitive task: widespread phase synchrony at all frequencies. *Clinical Neurophysiology* 120(4): 695–708.
Singer W (1998) Consciousness and the structure of neuronal representations. *Philosophical Transactions of the Royal Society London B Biological Science* 353(1377): 1829–1840.
Silvanto J, Lavie N, Walsh V (2005) Double Dissociation of V1 and V5/MT activity in visual awareness. *Cerebral Cortex* 15(11): 1736–1741.
Tong F (2003) Primary visual cortex and visual awareness. *Nature Reviews Neuroscience* 4(Mar): 219–229.
Tononi G (2008) Consciousness as integrated information: a provisional manifesto. *Biological Bulletin* 215(3): 216–242.
Tononi G, Koch C (2008) The neural correlates of consciousness. *Annals of the New York Academy of Sciences* 1124(1): 239–261.
Von Bonin G, Mehler W (1971) On columnar arrangement of nerve cells in cerebral cortex. *Brain Research* 27(1): 1–9.
Witzel C, Gegenfurtner KR (2018) Color perception: objects, constancy, and categories. *Annual Review of Vision Science* 4(Sep): 475–499.
Yu TL, Zeki S (2014) Perceptual asynchrony for motion. *Frontiers in Human Neuroscience* 8(Mar): 108.
Zeki S (2015a) Area V5—a microcosm of the visual brain. *Frontiers in Integrative Neuroscience* 9(21).
Zeki S (2015b) Review article: a massively asynchronous, parallel brain. *Philosophical Transactions of the Royal Society B: Biological Science* 370(1668).
Zeki S, Bartels A (1999) Toward a theory of visual consciousness. *Consciousness and Cognition* 8(2): 225–259.