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OPINION ARTICLE

REVISED The referential brain: why do some neurons learn and some do not? [version 2; peer review: 1 approved, 1 approved with reservations, 1 not approved]

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v2 First published: 26 May 2016, 5:1008
<https://doi.org/10.12688/f1000research.8809.1>
 Latest published: 28 Feb 2017, 5:1008
<https://doi.org/10.12688/f1000research.8809.2>

Abstract

Brain is phenomenally plastic and exhibits this capacity well into adulthood. Neuronal plasticity can be studied by using different adaptation protocols. Post-adaptation neurons typically show attractive and repulsive shifts even though challenged by the same adapter. Using orientation columns as a paradigm, we argue and suggest that repulsive shifts are essentially fundamental to preserve the functional organization of the cortex, and thus, maintaining the functional homeostasis of the brain.

Keywords

referential brain, repulsive shifts, attractive shifts, plasticity, visual cortex

Open Peer Review

Approval Status

	1	2	3
version 2 (revision) 28 Feb 2017			view
version 1 26 May 2016	view	view	
<ol style="list-style-type: none"> Jose Fernanado Maya-Vetencourt, Italian Institute of Technology (IIT), Genoa, Italy Stanislaw Glazewski, Keele University, Keele, UK Michael R. Ibbotson, Australian College of Optometry, Melbourne, Australia <p>Any reports and responses or comments on the article can be found at the end of the article.</p>			

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Competing interests: The authors declare no competing financial interests.

Grant information: The author(s) declared that no grants were involved in supporting this work.

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How to cite this article: Bharmauria V and Bachatene L. **The referential brain: why do some neurons learn and some do not?** [version 2; peer review: 1 approved, 1 approved with reservations, 1 not approved] F1000Research 2017, 5:1008
<https://doi.org/10.12688/f1000research.8809.2>

First published: 26 May 2016, 5:1008 <https://doi.org/10.12688/f1000research.8809.1>

REVISED Amendments from Version 1

As suggested by the reviewers, we have added an explanation on the role of refractory and repulsive neurons. Moreover, text related to the role of inhibitory neurons in maintaining this recalibration of orientation columns has also been added.

See referee reports

In daily life we use reference points to evaluate and analyse options around. Brain exhibits phenomenal plasticity during youth and even adulthood that helps animals adapt to different experiences (Bachatene *et al.*, 2015b; Dragoi *et al.*, 2001; Hensch, 2005; Kohn, 2007; Turrigiano & Nelson, 2004).

In general, neurons in the brain are selective to certain features. For example, a primary visual neuron (V1) is selective to a range of orientations (Hubel & Wiesel, 1962; Hubel & Wiesel, 1968; Swindale, 1998). Neuronal plasticity can be studied by employing several techniques and protocols (Kohn, 2007; Turrigiano & Nelson, 2004) such as visual deprivation and adaptation. Adaptation refers to the imposition of a non-optimal stimulus (adapter) within neuronal receptive fields for specific periods of time (usually several minutes) to alter their response behaviour (Kohn, 2007). Indeed, using various techniques in different brain areas, the effects of adaptation have been investigated on various neuronal properties such as orientation selectivity (Bachatene *et al.*, 2015b; Dragoi *et al.*, 2000; Gutnisky & Dragoi, 2008; Ghisovan *et al.*, 2009), motion (Kohn & Movshon, 2003), spatial frequency (Bouchard *et al.*, 2008; Marshansky *et al.*, 2011), and contrast (Baccus & Meister, 2002). After adaptation protocol, neurons typically show two types of behavioural shift patterns: attraction and repulsion. An attractive shift is the displacement of a tuning curve toward the adapter following adaptation, whereas a repulsive shift corresponds to the movement of the tuning curve away from the adapter. Some neurons refract the adapter and do not change their selectivity (Jeyabalaratnam *et al.*, 2013).

Interestingly, contingent upon the duration of stimulus, neurons may predominantly shift in one characteristic fashion. For example, a 3-min adaptation (Dragoi *et al.*, 2000) of visual neurons leads to a majority of repulsive shifts, whereas, a prolonged adaptation (> 6 min) potentiates attractive shifts (Bachatene *et al.*, 2015b; Cattani *et al.*, 2014; Ghisovan *et al.*, 2009). Why do some neurons learn and some do not, even though challenged by the same adapter? Does this apply to all the brain regions?

Here we put forth a concept through our recent results on the functional reprogramming of orientation columns in the visual cortex (Bachatene *et al.*, 2015b). In that report, we showed that neurons at the adapted and non-adapted cortical sites exhibited similar pattern of shifts. It is particularly interesting that the non-adapted neurons (not challenged by the adapter) also displayed changes in their orientation selectivity (they exhibited both types of shifts). This is illustrated as an example in Figure 1. The upper row displays a hypothetical layout of orientation columns in control conditions.

Figure 1. Functional reconfiguration of orientation columns post-adaptation. The upper row corresponds to the orientation layout of columns in the control (pre-adaptation) condition. The triangles show three distinct groups of neurons (with non-overlapping receptive fields) under observation within different columns. After an adaptation procedure (neurons in the red column, 90° , are adapted to 157.5°), the orientation layout of the columns is reconfigured (lower row). It is to be underlined that, although only neurons corresponding to 90° column were challenged by an adapter, neurons in other columns (non-adapted) also changed their selectivity. Two out of three neurons at the adapted site changed their selectivity toward the adapter, whereas one neuron shifted its selectivity away from the adapter. The repulsive neurons may have an important role to play in maintaining the functional dogma of orientation processing in the visual cortex. Note: Each colored sphere represents a neuron.

The activities of nine neurons under observation were recorded simultaneously that were tuned distinctly at each location (neurons at each location are linked by a black triangle; all three sites had non-overlapping receptive fields). After the adaptation procedure, neurons at each site changed their selectivity irrespective of the fact that only neurons tuned to 90° (pre-adaptation, red-columned neurons, middle triangle) were challenged with an adapter (157.5° degree orientation, purple bar). Notably, post-adaptation, two neurons (middle triangle, purple neurons) at the adapted site exhibited an attractive shift whereas one neuron displayed repulsion. In other words, only two neurons learnt the adapter whereas the third neuron swayed away from this behaviour. Interestingly, non-adapted neurons in other columns (left and right triangles) also displayed orientation selectivity shifts following adaptation.

Many reports (Bachatene *et al.*, 2013; Jia *et al.*, 2010; Wertz *et al.*, 2015) have shown and suggested that neuronal dendrites contain synapses corresponding to all the orientations. Within this framework, after a prolonged adaptation, the synapses representing the adapter would strengthen and become active, thus giving rise to a novel selectivity for the neuron. Therefore, new local networks are framed potentiating a changed column. Within this dynamic interplay, most local neurons may wire together and shift their responses in conjunction with each other toward the adapter whereas a minority may deflect away (repulsion) to participate in conservation of the columnar dogma. Few neurons may remain unaffected that are termed refractory neurons. Once this reference is set, other columns would systematically tilt to achieve their ultimate destiny without leaving an orientation hole. Therefore, repulsive neurons have a significantly equal role as attractive neurons to play in organizing principles of functional sensory processing. It has also been shown that putative fast-spiking neurons (inhibitory neurons) also exhibit shifts in their orientation tunings after adaptation protocols (Bachatene *et al.*, 2012; Chanauria *et al.*, 2016). Importantly, the inhibitory neurons which connect and regulate different brain areas (Das & Gilbert, 1995) maybe central to this robust recalibration of columnar organization. The pyramidal cells may first set the selectivity of neurons, wherein the interneurons regulate this selectivity on the local and distal (lateral) levels. Indeed, previous studies have suggested that repulsive neurons maybe implicated in improving the dissociation of different oriented gratings by reducing the response-redundancy of a population of orientation-selective neurons (Dragoi *et al.*, 2000; Hollmann *et al.*, 2015; Müller *et al.*, 1999). Although, repulsive shifts induced by short duration of adaptation (< 3min) durations have been suggested to occur as a consequence of an early mechanism comprising only response depression (Ghisovan *et al.*, 2009). Longer adaptation protocols (> 6 min) may even reverse the direction of these

shifts because of a late mechanism involving the response depression followed by response enhancement to the adapter (Ghisovan *et al.*, 2009). Biologically, this implies a homeostatic phenomenon allowing a sensory feature to conserve a basic state that will allow further plastic modifications (Bachatene *et al.*, 2015a; Turrigiano & Nelson, 2004). Thus, the cortical column is reframed with an equal representation of each optimal stimulus.

From the above paradigm, it is suggested that the brain, especially the cortex functions on such organizing principles. In fact, similarly to the visual cortex, distinct functional maps are present in other brain regions too. For example, the auditory cortex may also be functionally reorganized in such fashion (Nahum *et al.*, 2013). Although, neurons are arranged in a salt-and-pepper fashion in lower vertebrates, yet they exhibit selectivity to properties and may also reorganize through similar connectivity principles as higher vertebrates. Therefore, we suggest that neuronal functioning is referential in nature. This eventually facilitates the brain's ability to modify itself easily (plasticity), to form novel networks, and most importantly, to maintain the functional homeostasis.

Author contributions

VB wrote the manuscript. LB helped with critical remarks and manuscript writing. Both authors agreed to the final content of the article.

Competing interests

The authors declare no competing financial interests.

Grant information

The author(s) declared that no grants were involved in supporting this work.

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Open Peer Review

Current Peer Review Status:

Version 2

Reviewer Report 08 January 2019

<https://doi.org/10.5256/f1000research.11894.r41242>

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Michael R. Ibbotson

National Vision Research Institute (NVRI), Australian College of Optometry, Melbourne, Vic, Australia

This article is a brief essay that qualitatively describes how adaptation to a particular orientation in visual cortex may lead to changes in the orientation preferences of the cell population (and therefore the orientation preference maps). The description is purely qualitative, with no model presented, so it is hard to assess what contribution this makes to the literature. I had to read the two full papers cited by the authors to make any sense of this essay (by the way, those papers were worth the read). It is no surprise that adaptation at a particular orientation influences different cortical cells in different ways. Crowder *et al.* established that around 25% of cortical neurons adapt strongly even to orthogonal orientations that do not induce spiking in the recorded cell's themselves. Therefore, it is very well established that the cortical population has a wide range of adaptive characteristics, which will all contribute. It is also very well established that cortical columns are interconnected, so adaptation in one area is likely to influence other areas. Hietanen *et al.* also showed that the way cells adapt depends on where they are located in the orientation preference map. What is new about this article?

Some specific issues. The authors state "After adaptation protocol, neurons typically show two types of behavioural shift patterns: attraction and repulsion." This is a gross simplification. In fact there is a complex change in the response gain control mechanisms and very selective changes in the coding of most visual parameters. For example, contrast gain control changes the relationship between spike rate and stimulus contrast. Attractive and repulsive shifts in orientation tuning then lead on from these fundamental changes in the cell's responses based on the input from multiple cells in the population. No simple qualitative concept can capture this in a rigorous way without a mathematical model.

The authors state: "Some neurons refract the adapter and do not change their selectivity". What does it mean to "refract" the adapter?

The authors state "Many reports (Bachatene *et al.*, 2013; Jia *et al.*, 2010; Wertz *et al.*, 2015) have shown and suggested that neuronal dendrites contain synapses corresponding to all the

orientations." Care is needed here. There may be differences between mouse (with no orientation columns in V1) and cat cortex (which has orientation columns), so its difficult to generalise. I believe that extreme caution required in this paragraph.

On an editorial note, the essay needs a solid edit throughout, starting with the first sentence. In particular, the authors need to put articles where they are needed and remove them from where they are not.

Is the topic of the opinion article discussed accurately in the context of the current literature?

Partly

Are all factual statements correct and adequately supported by citations?

Partly

Are arguments sufficiently supported by evidence from the published literature?

Partly

Are the conclusions drawn balanced and justified on the basis of the presented arguments?

Partly

Competing Interests: No competing interests were disclosed.

Reviewer Expertise: Cortical visual physiologist

I confirm that I have read this submission and believe that I have an appropriate level of expertise to state that I do not consider it to be of an acceptable scientific standard, for reasons outlined above.

Version 1

Reviewer Report 06 February 2017

<https://doi.org/10.5256/f1000research.9483.r19937>

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Stanislaw Glazewski

School of Life Sciences, Keele University, Keele, UK

Bharmauria and Bachatene propose that the neurones termed "repulsive" (as they change their preferred orientation while challenged with the adaptor but do not follow it) are fundamental "to preserve the functional organisation of the cortex" or as it is found in a different place "to

participate in conservation of the columnar dogma". I neither recognise the arguments for this concept or the evidence that it is based on. Why would the presence of refractory neurones not be sufficient if any "columnar dogma" or "the reference" is required? Additionally, as the preferred orientation of neurones changes with the duration of adaptor presentation, it is plausible that the repulsive and even refractory neurones are still shifting to the adaptor's orientation. If the shifting is never absolute the remaining refractory and repulsive neurones could just have no function (noise). In any case the eventual function of refractory and repulsive neurones can be at present tested in small-scale experiment, as the appropriate technology is available. On the other hand, it would be much easier to test at first whether the repulsive and refractory neurones really exist (long adapting experiment) and if they are whether they are fixed at these functions (series of different adaptors' presentation experiment with use of the same population of neurones). The results should aid the concepts, which are premature at present.

Is the topic of the opinion article discussed accurately in the context of the current literature?

Partly

Are all factual statements correct and adequately supported by citations?

Partly

Are arguments sufficiently supported by evidence from the published literature?

Partly

Are the conclusions drawn balanced and justified on the basis of the presented arguments?

Partly

Competing Interests: No competing interests were disclosed.

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have significant reservations, as outlined above.

Author Response 22 Feb 2017

Vishal Bharmuria, Université de Montréal, Montréal, QC, Canada

We thank the reviewer for his comments on the manuscript. The comments of the reviewer have helped in clarification of the manuscript further. We have added a paragraph on the role of repulsive shifts. In fact, we have suggested this concept based on our recent findings (Bachatene *et al.* 2015b) on the visual cortex of the anaesthetized cat that such a phenomenon maybe occurring after adaptation procedures. We would like to emphasize that in addition to the neurons at the adapted site, neurons at the non-adapted sites also changed their selectivity. In fact, many reports (these papers have been cited in the article) have shown that refractory neurons exist in the cortex, however, refractory neurons and repulsive neurons could even reverse/change their orientation selectivity shift-directions toward the adapter after repetitive adaptations (Ghisovan *et al.* 2008). Indeed, neurons may be fixed at these functions, but only to a certain period of adaptation as they may change

their properties as the adapter duration is changed (Ghisovan *et al.* 2008). We have even tested shift amplitudes between 6 min until 24 min (Bachatene *et al.* 2015) of adaptation and the tested neurons always fall into three categories: attractive, repulsive and refractory neurons. However, longer adaptation protocols may potentiate attractive shifts in general. Although, the concept maybe premature at present but if one were to imagine the simultaneously recorded neurons from a column as an ensemble of neurons, the role of refractory neurons could be hypothesized as follows: There is plenty of evidence nowadays that in an ensemble of neurons, some neurons are strongly embedded in the circuits whereas others change their properties due to synaptic changes occurring at their dendrites. Such strongly embedded neurons may be compared to the refractory neurons, whereas others undergo change in their properties through short term plasticity. Indeed, further experiments could be designed to explore the exact roles of refractory neurons in circuits. However, within the framework of the columnar organization, they seem to be important in preserving this functional dogma.

Ghisovan *et al.* 2008. Visual Cells Remember Earlier Applied Target: Plasticity of Orientation Selectivity

Bachatene *et al.* (2015) Summation of connectivity strengths in the visual cortex reveals stability of neuronal microcircuits after plasticity. *BMC Neurosci.* 2015a;16:64. 26453336 10.1186/s12868-015-0203-1 4600218

Cossell *et al.* (2015) Functional organization of excitatory synaptic strength in primary visual cortex

Barth and Poulet (2012) [Experimental evidence for sparse firing in the neocortex](#)

Competing Interests: The authors declare no competing interests.

Reviewer Report 20 June 2016

<https://doi.org/10.5256/f1000research.9483.r14455>

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Jose Fernanado Maya-Vetencourt

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The manuscript by Bharmauria & Bachatene is a provocative opinion article that claims a role for a particular set of visual cortex neurons in mediating/maintaining some functional aspects of the organization of the visual cortex in response to external stimuli. The script is interesting, well

written, and reviews the pertinent literature. It is has potential implications in terms of neural circuitries computation of sensory information in the brain.

Using orientation columns as an experimental model, the authors propose that repulsive neurons may play an important role in the orientation processing by visual cortical neurons. The discussion is based on the emerging view that neuronal dendrites possess synapses corresponding to all orientation columns. The authors, however, fail to provide additional anatomical insights that may support their hypothesis. For instance, when thinking about neurons that learn orientation or repulsions shifts after adaptation, horizontal connections between spatially separated cortical areas represented by inhibitory interneurons that may ultimately influence synapses of dendrites of single units, immediately come to one's mind. Can the authors rule out this possibility? The work may also get insights from a description of experimental models designed to address the potential role of repulsive shifts in the preservation of the functional organization in the visual cortex.

Is the topic of the opinion article discussed accurately in the context of the current literature?

Partly

Are all factual statements correct and adequately supported by citations?

Partly

Are arguments sufficiently supported by evidence from the published literature?

Partly

Are the conclusions drawn balanced and justified on the basis of the presented arguments?

Partly

Competing Interests: No competing interests were disclosed.

I confirm that I have read this submission and believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.

Author Response 22 Feb 2017

Vishal Bharmuria, Université de Montréal, Montréal, QC, Canada

We thank the reviewer for his constructive comments on the manuscript. As suggested by the reviewer, we have added a paragraph that relates to the inhibitory neurons and horizontal connections in the cortex. Moreover, the role of repulsive neurons in maintaining the columnar organization after adaptation protocols, has also been added. We have also added a few references that suggest the role of repulsive neurons.

Competing Interests: The authors declare no competing interests.

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