Annotated Bibliography For HTM Researchers

Subutai Ahmad *
Numenta, Inc.
Redwood City, CA 94063
sahmad@numenta.com

Yuwei Cui
Department of Biology
University of Maryland
College Park, MD 20742
ywcui@umd.edu

Abstract

This document contains an annotated bibliography targeted towards those doing active research on Hierarchical Temporal Memory (HTM). The focus is on neuroscience, though there are occasional other references. The document consists of (possibly very brief) descriptions of specific papers. These descriptions emphasize on the relationship to HTM Theory and don't necessarily summarize the paper itself. There is typically exactly one paper, or a couple of tightly related papers, for each subsection. We hope the content is useful for finding appropriate citations when writing HTM related papers. The material could also be useful in understanding the neuroscience behind the HTM theory in more depth. The references section includes the abstracts for further details. The bibtex file for these references are exported from the public Mendeley HTM Neuroscience group.

Date: December 23, 2014

---

* Send all flames and blame to him.

Table of Contents

1 Neuroanatomy

As HTM is a theory of the neocortex, we focused on review papers on architecture of the mammalian cortex, including the laminar and columnar structures of the cortex and the thalamacortical circuits.

1.1 Thomson: Cortical anatomy

These papers by Thomson [30, 31, 29] are dense but contain a lot of detailed information about the connections into, out of, and within the various cortical layers and between different types of neurons in the cortex.

1.2 Buxhoeveden: minicolumn review

[6] Note from Jeff: *this is the best review article I know about mini-columns. Start here.*

The article also contains a bunch of data on typical measurements. From this you can gather that minicolumn widths vary quite significantly between species. The width can range from 20-60 microns, with about 40-80 microns distance in between (center to center). So there are 12 to 25 minicolumns per mm of cortex.

1.3 Constantinople and Bruno: parallel systems in the cortex

This recent paper by Constantinople and Bruno [8] challenged the classical belief of sensory processing pathway along $L4 \rightarrow L2/3 \rightarrow L5/6$ among cortical layers. Instead, it provided new evidence supporting the idea that superficial layers ($L4 \rightarrow L2/3$) and deeper layers (L5/6) act as parallel systems.

2 Sparse Distributed Representations

The HTM theory proposed that sparse distributed representations (SDRs) are used everywhere in the brain. In this section we summarized neuroscience research papers supporting this idea.

2.1 Olshausen: Sparse coding

The 1996, 1997 papers [21, 22] by Olshausen and Field represent the first computational papers on sparse representations in the cortex. Their work has been very influential in the machine learning and neuroscience. The 2004 paper [23] is shorter and easier to read, more of a review.

2.2 SDR object representations in IT

[13] is an extensive study of SDR-like properties in IT. They measured responses of 600 neurons in monkey IT to 1000 images. They analyzed the similarity between all pairs of responses. By doing agglomerative clustering they show that objects tend to cluster according to natural categories. i.e. similar objects have similar representations. They use many different distance methods, though only one is really shown in detail.

The selectivity of single cells was imperfect compared to cell population as a whole. Many cells discriminated between combinations of categories. In other words it is a distributed representation.

They showed that lower level simple and complex features (roughly equivalent to V1, V2) cannot account for these similarity metrics.

Note that each image was only presented for 105ms, so it's essentially a flash inference case.

2.3 SDR episodic memory in hippocampus

This paper [34] provides supporting evidence that a sparse distributed neural code is used for episodic memory in human hippocampus. Specifically, they showed that (i) a small percentage

of recorded neurons responded to any one target and (ii) a small percentage of targets elicited a strong response in any one neuron

2.4 Babadi: Sparseness and Expansion

The paper [2] is tangentially related to our SDR work. I am including it here only because we might want to cite it in our theory papers. I think there are several key differences:

- They are focused on sparseness combined with expansion. This is a bit strange, since expansion is not required and not found everywhere in the cortex.
- They require full connectivity matrix between the input layer and the encoding layer
- They are using analog weights and a very different distance function (Euclidean distance instead of overlap)

3 Pyramidal Neurons

Pyramidal neurons are the most numerous excitatory cells in the cortex and play important roles in advanced cognitive functions. This section contains research and review papers on properties of pyramidal neurons.

3.1 Spruston: Pyramidal neuron review

This paper [28] contains a very nice review of pyramidal neurons, including their various regions, active dendritic properties, number of synapses, etc. They focus on the commonalities across different cortical areas and hippocampus.

4 Active Dendrites

The HTM theory proposed that one important function of the neocortex is to generate predictions of what will happen in the future. Active dendritic properties are likely one of the underlying neural mechanisms of prediction and inference. In this section we reviewed supporting neuroscience evidences of active dendrites.

4.1 Antic: Decade of NMDA Spikes

From Jeff: *This is a short and relatively easy to read paper that covers the basics of NMDA dendritic spikes including some of the history. It might be a good introduction to the topic.*

The paper [1] describes evidence for the HTM "predictive state". A non-apical NMDA spike can depolarize a cell body (page 2998, middle of right column). The time course of this depolarization is interesting - the paper shows evidence for a more sustained depolarization than we typically model in HTMs. This could be used to help combat temporal noise or it could support the "learn on one cell" mode.

They also provide evidence that NMDA spikes are highly localized events incorporating a small dendritic segment. They are localized in space (10-40 microns) and localized in time. See page 2998, middle of left column.

4.2 Larkum: Synaptic integration in tuft dendrites

Although this paper [15] is primarily about apical tuft dendrites it is a good introduction to dendritic spikes in general, including basal dendrites. Figure 4H is a good summary diagram of how to think about a typical pyramidal neuron where the apical tuft dendrites act as a set of coincidence detectors similar to how the basal dendrites act as a set of coincidence detectors. The apical tuft dendrites generate a Ca spike and the basal dendrites generate a somatic Na action potential.

4.3 Branco: How dendritic segments integrate their inputs

This paper [5] contains some useful data on dendritic segments and how they integrate their inputs. Summary of findings:

1. Proximal dendrites sum over their synapses linearly. Synapses sum linearly and inputs must converge at the exact same time. They also show that more distal dendritic branches show threshold like (sigmoidal) response properties. This is nice confirmation for our model.

2. Distal dendrites have broader temporal integration windows. Quote: "We show that single cortical pyramidal cell dendrites exhibit a gradient of temporal summation and input gain that increases from proximal to distal locations. This suggests a progressive shift of computational strategies for synaptic inputs along single dendrites.

   Near the base if inputs are more than a few msecs apart, the evoked potential drops significantly. Confirmation that proximal dendrites act as coincidence detectors. Segments farther away from the base can sum over longer temporal intervals. At the most distal locations, evoked potential stays constant for much longer than 10 msecs.

   Another way to phrase this is that proximal segments require precise synchrony (coincidence detection), distal segments do not require such precise timing.

3. More distal segments have higher gain (sigmoid gain) and require fewer synapses to fire. As a consequence, they also state that really distal segments can be as effective or even more effective than proximal dendrites in driving axonal output. Not sure what to make of this.

4. They show all this in Layer 2/3 as well as Layer 5 pyramidal cells.

Some reactions to temporal property: We don't model the timing property of distal segments today, but this property could be very useful. For example longer temporal scales can be helpful in dealing with temporal noise. A longer scale will make us more resistant to temporal insertions. It could also be used to create connections from a single segment to time steps t-1 and t-2. This will make us more robust to temporal deletions. (This is similar to our old pooling idea.)

Distal inputs into L4 can be coming in at different time scales (motor commands could be slower than sensory input). A longer temporal integration period may be necessary for proper sensorimotor inference.

If apical dendrites have much larger temporal integration windows, this could be very useful for feedback which necessarily has a slower time scale.

4.4 Major: Active properties of dendrites

This paper [17] cites evidence that distal dendritic spikes often have a weaker modulatory effect. (Proximal connections are thought to have a stronger effect.)

They review different types of cell models.

They provide numbers regarding the minimum number of synapses required to trigger dendritic spikes that match up very well with our formal analysis of SDRs. NMDA spike in distal dendrites can be evoked by as few as 10 active synapses that are clustered together (page 17, top left).

4.5 Larkum: BAC firing hypothesis

Feedback input to apical dendrites by themselves can cause strong action potentials. If it is coincident with matching feed forward input, the cell bursting can be sustained for a period of time. This can happen if apical input is coincident with matching feed forward input. Mechanisms for that are reviewed. Figure 3a is an example of this.

...this article [14] has dealt with the biophysical evidence for the existence of an associative firing mechanism in pyramidal neurons and its influence on the input/ output function. This degree of integration between the micro- and macroarchitecture, as well as inbuilt complexity at the cellular level, invites speculation about whether and how the whole system utilizes this feature. The importance of this mechanism conceptually is that the pyramidal neuron is able to detect coincident input to

proximal and distal dendritic regions, investing the cortex with an inbuilt associative mechanism at the cellular level for combining feed-forward and feedback information.

The BAC firing hypothesis presented here offers a cellular mechanism that addresses a number of questions about the cortex. It suggests that the pyramidal neuron cell type is an associative element which carries out the same essential task at all cortical stages: that of coupling feed-forward and feedback information at the cellular level.

Martinotti neurons blocking dendritic activity - what is this for? Need to review. Could this turn off pooling when columns burst?

4.6 Yang: Branch specific dendritic learning

This amazing paper [36] studies learning on specific dendritic branches in awake rats while they go through normal behavior. It shows learning induced dendritic branch specific formation of synapses, which is consistent with the temporal memory algorithm and high order sequences. This paper deals with high order motor sequences. Ignore the sleep part.

4.7 Palmer: NMDA Spikes

Few papers talk about dendritic NMDA spikes in Layer 2/3 pyramidal neurons. That is the topic of this paper [24] showing that Layer 2/3 cells act similarly to the more studied L5 and Hippocampal Ca1 pyramidal neurons.

5 Synapses and Plasticity

Learning requires changes of synaptic connections between neurons. In this section we reviewed papers on synaptic plasticity, with a focus on experience-dependent formation and elimination of synapses.

5.1 Chklovskii: Potential synapses

This paper [7] includes evidence and arguments for dynamic synapse formation, potential synapses, etc. Jeff says on the NuPIC Theory mailing list:

Classic Hebbian learning is about strengthening synapses, but we are suggesting that new synapses are formed. I think you are asking how this is possible biologically. The idea for potential synapses comes from a researcher Chklovskii. An axon and dendrite that are near each other but that are not connected can still sense pre- and post-syaptic activity and this is sufficient for them to start to grow a new synapse when they are active at the same time. What is actually is grown is a spine that connects the axon and dendrite. The synapse is on the end of the spine. In addition, glial cells have been shown to act as intermediaries. They can encourage a dendrite and axon to move/grow closer together when they fire at the same time. Glial cells effectively increase the number of potential synapses. Finally, the ends of the dendritic and axonal tress are constantly growing I different directions trying to find new useful connections. It is now well known that synapses and spines form during learning and they also disappear. This can happen rapidly, in a matter of minutes in some cases.

I believe the concept of potential synapses and the growth of new synapses applies to both proximal and distal synapses. In our temporal memory implementation we decided to implement it differently purely to make the software more efficient and to use less memory. Instead of maintaining a large pool of potential synapses, most of which would have 0 permanence, we choose from the set of active cells.

5.2 Experience-dependent synaptogenesis

The review paper by Bailey and Kandel [3] presents numerous early researches supporting synapse formation during formation of long-term memory.

Zito and Svoboda 2002 [37] is a short review of activity-dependent synaptogenesis in the adult cortex. This review first presented the common view of synaptic plasticity, which argues initial establishment of synaptic connections occurs independent of learning, and experience refines existing synaptic connections, rather than create new ones (para 2, page 1). Zito and Svoboda then presented a different view, which argues "short-term plasticity depends on existing synapses, but long term changes in synaptic strength are accompanied by structural rearrangements, through formation or elimination of synapses. This second view is consistent with the current HTM algorithms.

A more recent review paper by Holtmaat and Svoboda [11] presents more recent findings with imaging techniques. I find the numbers in supplementary table S1 very useful, it shows what fraction of synapses are stable from many different studies.

5.3 Imaging the growth of synapses

Most recent studies are use fancy image techniques to study synapse formation. Trachtenberg et al [32] first shows experience-dependent synapse formation and elimination with long-term imaging. Niell et al. [20] contains a movie showing how fast synapses and dendritic segments can change dramatically within 24 hours.

6 Sequence Learning

In this section we reviewed evidence of sequence learning in the cortex. One prediction of the HTM theory is unexpected input will cause bursting activities in the cortex whereas predicted inputs are represented by SDRs. The other prediction is formation and elimination of lateral connections between neurons are the underlying mechanism of sequence learning. These predictions are supported by the following studies.

6.1 Vinje and Gallant: Temporal sequences are sparser

Part of a classic set of studies for HTM sequence learning. This paper [33] demonstrates increasingly sparse neural activity when a neuron gets larger spatio-temporal context compared to flash input. Moreover the same set of neurons tend to fire given the same temporal context. (They show temporal context by creating that simulate eye saccades.)

There are some problems with the study. For one, the eye movements are not initiated by the monkey. Instead the movie simulates what the monkey might see during saccades. This is a huge issue. Their analysis also assumes there are no temporal correlations in neural activity. Another big problem since temporal pooling creates temporal correlations. They don't really think in terms of the monkey learning sequences. Etc.

6.2 Milier: Visual stimuli recruit intrinsically generated cortical ensembles

This paper [19] provides some supporting evidence of the Temporal Memory algorithm.

Neuroscientists traditionally think that neurons in the cortical encode sensory stimulus individually: each neuron has some preferred stimulus, which can be measured through receptive field (RF) mapping. When a stimulus comes in, a neuron will fire if it matches its RF well, and will stay silent otherwise.

What's interesting in this paper is that the authors suggest groups (ensembles) of neurons , rather than individual neurons, are the functional units of cortical activity. When a stimulus is presented, cortical activity is dominated by coactive groups of neurons. Presumably these ensembles are supported via learned recurrent excitatory connections, since they also appears during spontaneous activity.

I find this consistent with the temporal memory algorithm (previously known as the CLA algorithm), which suggest external stimulus triggers a unique sequence of cells, which are connected via lateral connections. However, the technology used in this paper (two-photon imaging) has a relatively poor temporal resolution, so it is not possible to tell whether the "coactive group of neurons" fires sequentially or simultaneously.

Chetan: What else is interesting is that they found single neurons to participate in multiple ensembles, regardless of how specialized they were for a stimulus at an individual level. (See section titled "Single Neurons Participate Promiscuously in Multiple Ensembles").

Also, this is interesting: "Taken together, our findings demonstrate that when individual neurons are activated, they are more likely to be activated together with a specific set of other neurons as an ensemble. At the same time, individual neurons can participate in multiple ensembles, dynamically reorganizing their allegiance with different sets of neurons."

6.3 Meyer: surprise responses in IT

Subutai: Ive been trying to locate strong experimental evidence that surprise inputs result in cells in mini column firing (aka bursting). The attached paper doesnt quite show that, but it has some other relevant information [18]. Unpredicted stimuli elicits a stronger response in IT than predicted stimuli. The mean firing rate of neurons is higher with unpredicted stimuli (Figure 2). In figure 2A you do see a slightly increased mean response rate to predicted stimuli (above baseline) but the average response is higher for unpredicted stimuli. All this is consistent with column bursting in temporal memory. In this paper you can't tell whether the surprise is along a minicolumn or not. Additional experiments showed that unpredicted firing had slightly longer latency than predicted firing. This is consistent with predicted cells firing earlier due to depolarization. Predicted firing was about 5 msecs faster than unpredicted firing, which is also about what you would expect.

6.4 Fishman: Oddball responses in auditory cortex

From EEG recordings, people know that unexpected stimulus ("deviant" sounds in this study), will elicit stronger response. This paper [10] studies the neural mechanisms and brain regions underlying this effect in the primary auditory cortex. They confirmed that spiking response were larger when elicited by the unexpected stimulus, and the difference between expected and unexpected stimulus were more prominent in later activity. The unexpected stimulus can be introduced either in a oddball paradigm in which rare deviant tones are randomly interspersed among frequent standard tones (Fig. 1B), or in a random sequence where tone is unexpected (Fig. 1C).

One downside of this study is they used a very simple sequence for the oddball paradigm. It will be more interesting to see whether the same phenomenon holds when they play a more complex tone sequence (an oddball within a melody). They conclude that the difference between unexpected stimulus and repeated expected stimulus is due to stimulus specific adaptation (rather than prediction).

7 Temporal Pooling and Invariances

The idea of temporal pooling propose that after learning, predicted inputs will lead to stable (invariant) representations in higher levels of the cortical hierarchy despite changes of inputs at lower levels of the hierarchy. We summarized supporting neuroscience evidences for this idea below.

7.1 Li and DiCarlo: Learning invariances

This paper [16] very closely supports HTM temporal pooling ideas, including the role of sensorimotor inference in forming invariant representations. A detailed summary follows:

They found neurons in monkey IT that responded strongly to a particular object P (preferred) and moderately to another N (non-preferred). Tested position tolerance of these objects to get a baseline. The difference between the responses to P and N is the selectivity for this neuron. They did this for about 100 neurons in two monkeys, and many different objects.

They then altered temporal contiguity of stimuli and tested the effects on these invariant representations.

In the experiment, monkeys viewed altered stimuli for several hours. Basically there were three positions for each object: centered, 3 above and below. For a given P object, the position above or below was designated the swap position. As eyes moved around, a P object would be shown in the swap position but was was replaced by the N object during saccade. (Each saccade lasts 23 msecs.)

This would happen every time P object was shown in the swap position. A P object in the non-swap position didnt change when the money saccaded. (The swap position was randomly changed for different objects.) The monkey is effectively blind during a saccade, so they dont see the change - they just see the new object after fixation.

Their prediction: invariance selectivity at swap position would change. Selectivity in the non-swap position wont change. This is what happened. At swap position cells did not discriminate as well between P and N. Neuron became more responsive to N and less responsive to P, but only at that location. Change was location specific and shape specific, so very specific to this particular invariance. These changes cannot be explained by attention affects or retinotopic adaptation (everything was counter balanced).

However another paper of theirs seemed to indicate that temporal contiguity alone was not enough. Looks like eye movements may also be required (this is their reference 10 - Cox and DiCarlo, 2005. Attached paper 2).

They call this effect Unsupervised temporal tolerance learning or UTL. This is just temporal pooling for us. The behavior they describe is exactly the pooling behavior we would expect in layer 3.

In [9] they have the same experiment as [16], but here they used human subjects and a same-difference psychological test. Swapped objects were much more likely to be confused than non-swapped objects. They did the same experiment without eye saccades, and did not see the effect.

"Moreover, the confusions are predictable in that they are what is expected if the visual system assumes that object identity is stable across the short time interval of a saccade."

7.2 Isik et al: Learning invariance using temporal associations

Yuwei: Here [12] is a modeling study from Tomaso Poggio's lab that is very relevant to the idea of temporal pooling. This paper aims to explain the "invariance disruption" experiments, which is the study Subutai found that supports temporal pooling. In that experiment, Li and DiCarlo [16] showed that individual IT neurons change their selectivity in a position-dependent manner after exposure to the altered visual experiment. The modeling study here used a temporal association learning rule to learn transformation invariance through natural visual experience. The basic underlying idea is very similar to temporal pooling: since the external visual scene usually changes at a slow time scale, "temporal adjacency" is a good cue that two images are of the same object.

I think the major difference between this study and what we have is they don't distinguish between predicted and unpredicted inputs. In our algorithm, we only start temporal pooling when the input is predicted. They also don't have a motor component in their model. Nevertheless, I feel this line of study (developing invariance with temporal association rules) is very relevant for us to think about temporal pooling. i am planning to take a look at some papers along these lines.

Jeff: In addition to Yuwei's observations I would add: - They make a distinction between generic transformations (such as image translations) and class-specific translations (such as rotation through plane). They argue that generic transformations apply to all objects but class-specific transformations do not. I am struggling to see if this distinction really exists. I would prefer that temporal pooling works the same in all cases and that this distinction doesn't exist.

Another thing they talk about which I found odd is they ask, why should training continue throughout life? They say generic transformations can be set early in life. This seems ridiculous to me. Perhaps they are trying to show that HMAX (which doesn't learn at all) is a good model. They show a chart (figure 2) showing that for translation fixed HMAX is as good as learning temporal pooling.

8 Thalamocortical Pathways

8.1 Sherman and Guillery: The Book

For those interested in going deeper into the role of the thalamus, this is an excellent book [26]. Suggested by Jeff, it is a well written summary of a modern view of cortico-thalamic connections. It describes, for example, the connections between every cortical region and the thalamus including

the role of sub-cortical motor centers. It does require some neuroscience background but is much easier to read than many of the really dense neuroscience papers. The diagrams are also very clear.

9   Sensorimotor Inference

The idea of sensorimotor inference proposed cortex makes prediction of future inputs based on both the current inputs and a copy of motor command that is about to be executed. Some supporting evidences are summarized below.

9.1   Bartoli: SDR representations of tools

This paper [4] is concerned with merging of information from visual properties of tools to the motor coordinates for using and interacting with those tools. Looking at premotor and motor populations of neurons coding for specific hand configurations.

An "affordance" is the set of stuff that can be done to an object. It is the possibility of some actions that can be performed on an object.

Neurons in premotor cortex code for object specific and grip specific actions. (Rochat, 2010). A subset of these neurons fire for executing a specific hand-object and a specific visual representation of that object. (Murata 97) This activity is indepedient of whether that action actually occurs later.

This paper shows that the same specific patterns observed in monkeys also occurs in humans. They visually show specific tools to people, and observe very specific "motor plans" arising as a result of the stimuli. The main contribution is to "close the gap" between monkey and human data. In addition, they show that very specific visuomotor representations can form in humans as soon as 150 msecs after visual presentation of the object. The did a TMS study, so the stimulated premotor cortex (they did not perform direct neural recordings). They did record activity from hand muscles.

9.2   Wolpert: Forward models

This paper [35] discussed sensorimotor inference from a computational perspective. They proposed a forward model that uses the current state of the motor system and motor command to predict the next state. This is similar to our sensorimotor inference algorithms. The forward model concept in this paper is widely used in motor control and sensorimotor inference.

9.3   Sommer: Efference Copy

This review paper [27] summarizes a series of studies that established a pathway for corollary discharge signal (the motor command copy to sensory cortex), explains how predictive shifting of receptive field is constructed with CD signal, and how visual stability is achieved despite eye-movements.

10   Related Computational Models

In this section we reviewed several computational models that is related to the HTM theory.

10.1   Rinkus - The Sparsey model

I have read through the paper [25] and summarized some relevant points below. I tried to do this by focusing on the ideas instead of the algorithm details (which I am still struggling with). It is indeed a hard paper to read. The author is writing in his own language and often refer to terms not defined yet in the text. It is more like a technical report than a well-written journal article (a very bad introduction at the beginning). Nevertheless, I think some of the ideas presented in this paper are nice and largely consistent with what we have now.

Overall Goal

I think it might be good to state the goal of this work at the beginning, which is somewhat similar to ours. First, it is desired to have the ability to form large numbers of permanent memory traces of arbitrary spatiotemporal events on-the-fly and based on single trials. Second, the ability to subsequently directly, without serial search, retrieve the best-matching memory given an input, this retrieval should be invariance to nonlinear time-warping (i.e., if you speed up or slow down the input nonlinearly). Finally, the author also want the algorithm to be somewhat biologically plausible, relying on Hebbian-like learning rules rather than gradient calculation like deep-learning approaches.

Sparse Distributed Code (SDC).

This is the key component of the entire paper. The author has a good understanding on this topic and proposed something very similar to our algorithm: SDC must be used everywhere along the cortical hierarchy. The author provides many neuroscience evidences supporting this idea (e.g., right bottom of Page 6 on SDC in IT), and compares localist codes used in the HMAX framework with the SDC (Fig I-4, the section Sparse distributed codes and Localist Codes at bottom of Page 7, and discussion on Page 40-41). I think this is a good paper to cite for Subutai's SDR paper. Some similar points are made with SDC, such as why this is important for from a capacity point of view.

Macrocolumn, ("MAC").

The author acknowledged the existence of mini-columns (which he refers as "competitive-modules", or CM), but he focused on macro-columns as the basic coding unit in his algorithm. I find the definition of MAC fuzzy and somewhat arbitrary. It is basically a collection of ~70 minicolumns and correspond to "hypercolumns" in V1. I think we can get something similar by having topology turned on in our algorithms. Nevertheless, this design forced one to think in terms of distributed representation, rather than individual cells. The author had an interesting discussion on a novel concept of "receptive field of a MAC as a whole" at the bottom of Page 3.

Contextual input from horizontal and feedback connections.

This is another advance over the HMAX framework and is consistent with our algorithm. There are three sets of inputs to each MAC: bottom-up (U), horizontal (H), and top-down (D) inputs. Each MAC combines the three inputs to yield a scalar judgement G, which represents the familiarity of the current input (bottom of page 2) and can be used for retrieval/recognition purpose. At first glance, I don't think this is a biologically plausible operation as it depends on the global state of a MAC, but maybe some local neural network mechanism can do that. Nevertheless, the inclusion of contextual inputs makes the algorithms suitable for "sequence memory"

Code Selection Algorithm.

During the learning, the key problem is how to choose a SDC code for each MAC given the current input. The goal is to achieve a similar inputs map to similar codes (SISC) principle (Fig. I-6), just like what we what to achieve with the spatial pooling algorithm. The novel part of his algorithm is contextual inputs are also considered during spatial pooling (now I am using our terminology). The idea is to extend the similarity metric to multiplicatively combine overlap similarity metrics of the U, H and D inputs.

Invariance to nonlinear time warping

This is temporal noise in our terms. As stated in 0, one of the goals in this paper is to address the nonlinear time warping problem (e.g., consider inputs [BOUNDARY], [BOUNDRY] and [BOUNNNNNNDARY], should they be regarded the same?). The problem is addressed by a trick. At each step, a mac computes a series of estimates of the match of the current temporal-context-dependent input not just to the set of actual moments it experienced during learning (which constitute its explicit spatiotemporal basis), but to a much larger space of variants of the basis moments that were not actually experienced (see Discussion on Page 22). Personally I don't think this is a great solution, but could be food for thoughts when we are working on the temporal noise problem.

References

[1] Srdjan D. Antic, Wen Liang Zhou, Anna R. Moore, Shaina M. Short, and Katerina D. Ikonomu. The decade of the dendritic NMDA spike, 2010.

Abstract: *In the field of cortical cellular physiology, much effort has been invested in understanding thick apical dendrites of pyramidal neurons and the regenerative sodium and calcium spikes that take place in the apical trunk. Here we focus on thin dendrites of pyramidal cells (basal, oblique, and tuft dendrites), and we discuss one relatively novel form of an electrical signal ("NMDA spike") that is specific for these branches. Basal, oblique, and apical tuft dendrites receive a high density of glutamatergic synaptic contacts. Synchronous activation of 10-50 neighboring glutamatergic synapses triggers a local dendritic regenerative potential, NMDA spike/plateau, which is characterized by significant local amplitude (40-50 mV) and an extraordinary duration (up to several hundred milliseconds). The NMDA plateau potential, when it is initiated in an apical tuft dendrite, is able to maintain a good portion of that tuft in a sustained depolarized state. However, if NMDA-dominated plateau potentials originate in proximal segments of basal dendrites, they regularly bring the neuronal cell body into a sustained depolarized state, which resembles a cortical Up state. At each dendritic initiation site (basal, oblique, and tuft) an NMDA spike creates favorable conditions for causal interactions of active synaptic inputs, including the spatial or temporal binding of information, as well as processes of short-term and long-term synaptic modifications (e.g., long-term potentiation or long-term depression). Because of their strong amplitudes and durations, local dendritic NMDA spikes make up the cellular substrate for multisite independent subunit computations that enrich the computational power and repertoire of cortical pyramidal cells. We propose that NMDA spikes are likely to play significant roles in cortical information processing in awake animals (spatiotemporal binding, working memory) and during slow-wave sleep (neuronal Up states, consolidation of memories).*

[2] Baktash Babadi and Haim Sompolinsky. Sparseness and Expansion in Sensory Representations. *Neuron*, 83(5):1213–1226, August 2014.

Abstract: *In several sensory pathways, input stimuli project to sparsely active downstream populations that have more neurons than incoming axons. Here, we address the computational benefits of expansion and sparseness for clustered inputs, where different clusters represent behaviorally distinct stimuli and intracluster variability represents sensory or neuronal noise. Through analytical calculations and numerical simulations, we show that expansion implemented by feed-forward random synaptic weights amplifies variability in the incoming stimuli, and this noise enhancement increases with sparseness of the expanded representation. In addition, the low dimensionality of the input layer generates overlaps between the induced representations of different stimuli, limiting the benefit of expansion. Highly sparse expansive representations obtained through synapses that encode the clustered structure of the input reduce both intrastimulus variability and the excess overlaps between stimuli, enhancing the ability of downstream neurons to perform classification and recognition tasks. Implications for olfactory, cerebellar, and visual processing are discussed.*

Tags: Neuroscience,SDR

[3] C H Bailey and E R Kandel. Structural changes accompanying memory storage. *Annual review of physiology*, 55:397–426, January 1993.

Tags: Synapses

[4] Eleonora Bartoli, Laura Maffongelli, Marco Jacono, and Alessandro D'Ausilio. Representing tools as hand movements: early and somatotopic visuomotor transformations. *Neuropsychologia*, 61:335–44, August 2014.

Abstract: *The term affordance defines a property of objects, which relates to the possible interactions that an agent can carry out on that object. In monkeys, canonical neurons encode both the visual and the motor properties of objects with high specificity. However, it is not clear if in humans exists a similarly fine-grained description of these visuomotor transformations. In particular, it has not yet been proven that the processing of visual features related to specific affordances induces both specific and early visuomotor transformations, given that complete specificity has been reported to emerge quite late (300-450ms). In this study, we applied an adaptation-stimulation paradigm to investigate early cortico-spinal facilitation and hand movements synergies evoked by the observation of tools. We adapted, through passive observation of finger movements, neuronal populations coding either for precision or power grip actions. We then presented the picture of one tool affording one of the two grasps types and applied single-pulse Transcranial Magnetic Stimulation (TMS) to the hand primary motor cortex, 150ms after image onset. Cortico-spinal excitability of the Abductor Digiti Minimi*

and Abductor Pollicis Brevis showed a detailed pattern of modulations, matching tools affordances. Similarly, TMS-induced hand movements showed a pattern of grip-specific whole hand synergies. These results offer a direct proof of the emergence of an early visuomotor transformation when tools are observed, that maintains the same amount of synergistic motor details as the actions we can perform on them.

Tags: Sensorimotor Inference

[5] Tiago Branco and Michael Häusser. Synaptic integration gradients in single cortical pyramidal cell dendrites. *Neuron*, 69(5):885–92, March 2011.

> **Abstract:** *Cortical pyramidal neurons receive thousands of synaptic inputs arriving at different dendritic locations with varying degrees of temporal synchrony. It is not known if different locations along single cortical dendrites integrate excitatory inputs in different ways. Here we have used two-photon glutamate uncaging and compartmental modeling to reveal a gradient of nonlinear synaptic integration in basal and apical oblique dendrites of cortical pyramidal neurons. Excitatory inputs to the proximal dendrite sum linearly and require precise temporal coincidence for effective summation, whereas distal inputs are amplified with high gain and integrated over broader time windows. This allows distal inputs to overcome their electrotonic disadvantage, and become surprisingly more effective than proximal inputs at influencing action potential output. Thus, single dendritic branches can already exhibit nonuniform synaptic integration, with the computational strategy shifting from temporal coding to rate coding along the dendrite.*

Tags: Neuroscience,Sequence Learning

[6] D. P. Buxhoeveden. The minicolumn hypothesis in neuroscience. *Brain*, 125(5):935–951, May 2002.

> **Abstract:** *The minicolumn is a continuing source of research and debate more than half a century after it was identified as a component of brain organization. The minicolumn is a sophisticated local network that contains within it the elements for redundancy and plasticity. Although it is sometimes compared to subcortical nuclei, the design of the minicolumn is a distinctive form of module that has evolved specifically in the neocortex. It unites the horizontal and vertical components of cortex within the same cortical space. Minicolumns are often considered highly repetitive, even clone-like, units. However, they display considerable heterogeneity between areas and species, perhaps even within a given macrocolumn. Despite a growing recognition of the anatomical basis of the cortical minicolumn, as well as its physiological properties, the potential of the minicolumn has not been exploited in fields such as comparative neuroanatomy, abnormalities of the brain and mind, and evolution.*

Tags: Anatomy,Neuroscience

[7] D B Chklovskii, B W Mel, and K Svoboda. Cortical rewiring and information storage. *Nature*, 431(7010):782–8, October 2004.

> **Abstract:** *Current thinking about long-term memory in the cortex is focused on changes in the strengths of connections between neurons. But ongoing structural plasticity in the adult brain, including synapse formation/elimination and remodelling of axons and dendrites, suggests that memory could also depend on learning-induced changes in the cortical 'wiring diagram'. Given that the cortex is sparsely connected, wiring plasticity could provide a substantial boost in storage capacity, although at a cost of more elaborate biological machinery and slower learning.*

Tags: Neuroscience,Synapses

[8] Christine M Constantinople and Randy M Bruno. Deep cortical layers are activated directly by thalamus. *Science (New York, N.Y.)*, 340(6140):1591–4, June 2013.

> **Abstract:** *The thalamocortical (TC) projection to layer 4 (L4) is thought to be the main route by which sensory organs communicate with cortex. Sensory information is believed to then propagate through the cortical column along the L4L2/3L5/6 pathway. Here, we show that sensory-evoked responses of L5/6 neurons in rats derive instead from direct TC synapses. Many L5/6 neurons exhibited sensory-evoked postsynaptic potentials with the same latencies as L4. Paired in vivo recordings from L5/6 neurons and thalamic neurons revealed substantial convergence of direct TC synapses onto diverse types of infragranular neurons, particularly in L5B. Pharmacological inactivation of L4 had no effect on sensory-evoked synaptic input to L5/6 neurons. L4 is thus not an obligatory distribution hub for cortical activity, and thalamus activates two separate, independent "strata" of cortex in parallel.*

[9] David D Cox, Philip Meier, Nadja Oertelt, and James J DiCarlo. 'Breaking' position-invariant object recognition. *Nature neuroscience*, 8:1145–1147, 2005.

> **Abstract:** *While it is often assumed that objects can be recognized irrespective of where they fall on the retina, little is known about the mechanisms underlying this ability. By exposing human subjects to an altered world where some objects systematically changed identity during the transient blindness that accompanies eye movements, we induced predictable object confusions across retinal positions, effectively 'breaking' position invariance. Thus, position invariance is not a rigid property of vision but is constantly adapting to the statistics of the environment.*

> **Tags:** Neuroscience,Temporal Pooling

[10] Yonatan I Fishman and Mitchell Steinschneider. Searching for the mismatch negativity in primary auditory cortex of the awake monkey: deviance detection or stimulus specific adaptation? *The Journal of neuroscience : the official journal of the Society for Neuroscience*, 32:15747–58, 2012.

> **Abstract:** *The mismatch negativity (MMN) is a preattentive component of the auditory event-related potential that is elicited by a change in a repetitive acoustic pattern. While MMN has been extensively used in human electrophysiological studies of auditory processing, the neural mechanisms and brain regions underlying its generation remain unclear. We investigate possible homologs of the MMN in macaque primary auditory cortex (A1) using a frequency oddball paradigm in which rare "deviant" tones are randomly interspersed among frequent "standard" tones. Standards and deviants had frequencies equal to the best frequency (BF) of the recorded neural population or to a frequency that evoked a response half the amplitude of the BF response. Early and later field potentials, current source density components, multiunit activity, and induced high-gamma band responses were larger when elicited by deviants than by standards of the same frequency. Laminar analysis indicated that differences between deviant and standard responses were more prominent in later activity, thus suggesting cortical amplification of initial responses driven by thalamocortical inputs. However, unlike the human MMN, larger deviant responses were characterized by the enhancement of "obligatory" responses rather than the introduction of new components. Furthermore, a control condition wherein deviants were interspersed among many tones of variable frequency replicated the larger responses to deviants under the oddball condition. Results suggest that differential responses under the oddball condition in macaque A1 reflect stimulus-specific adaptation rather than deviance detection per se. We conclude that neural mechanisms of deviance detection likely reside in cortical areas outside of A1.*

> **Tags:** Auditory,Sequence Learning

[11] Anthony Holtmaat and Karel Svoboda. Experience-dependent structural synaptic plasticity in the mammalian brain. *Nature reviews. Neuroscience*, 10(9):647–58, September 2009.

> **Abstract:** *Synaptic plasticity in adult neural circuits may involve the strengthening or weakening of existing synapses as well as structural plasticity, including synapse formation and elimination. Indeed, long-term in vivo imaging studies are beginning to reveal the structural dynamics of neocortical neurons in the normal and injured adult brain. Although the overall cell-specific morphology of axons and dendrites, as well as of a subpopulation of small synaptic structures, are remarkably stable, there is increasing evidence that experience-dependent plasticity of specific circuits in the somatosensory and visual cortex involves cell type-specific structural plasticity: some boutons and dendritic spines appear and disappear, accompanied by synapse formation and elimination, respectively. This Review focuses on recent evidence for such structural forms of synaptic plasticity in the mammalian cortex and outlines open questions.*

> **Tags:** Synapses

[12] Leyla Isik, Joel Z Leibo, and Tomaso Poggio. Learning and disrupting invariance in visual recognition with a temporal association rule. *Frontiers in computational neuroscience*, 6:37, January 2012.

> **Abstract:** *Learning by temporal association rules such as Foldiak's trace rule is an attractive hypothesis that explains the development of invariance in visual recognition. Consistent with these rules, several recent experiments have shown that invariance can be broken at both the psychophysical and single cell levels. We show (1) that temporal association learning provides appropriate invariance in models of object recognition inspired by the visual cortex, (2) that we can replicate the "invariance disruption" experiments using these models with a temporal association learning rule to develop and maintain invariance, and (3) that despite dramatic*

single cell effects, a population of cells is very robust to these disruptions. We argue that these models account for the stability of perceptual invariance despite the underlying plasticity of the system, the variability of the visual world and expected noise in the biological mechanisms.

Tags: Temporal Pooling

[13] Roozbeh Kiani, Hossein Esteky, Koorosh Mirpour, and Keiji Tanaka. Object category structure in response patterns of neuronal population in monkey inferior temporal cortex. *Journal of neurophysiology*, 97:4296–4309, 2007.

Abstract: *Our mental representation of object categories is hierarchically organized, and our rapid and seemingly effortless categorization ability is crucial for our daily behavior. Here, we examine responses of a large number (¿600) of neurons in monkey inferior temporal (IT) cortex with a large number (¿1,000) of natural and artificial object images. During the recordings, the monkeys performed a passive fixation task. We found that the categorical structure of objects is represented by the pattern of activity distributed over the cell population. Animate and inanimate objects created distinguishable clusters in the population code. The global category of animate objects was divided into bodies, hands, and faces. Faces were divided into primate and nonprimate faces, and the primate-face group was divided into human and monkey faces. Bodies of human, birds, and four-limb animals clustered together, whereas lower animals such as fish, reptile, and insects made another cluster. Thus the cluster analysis showed that IT population responses reconstruct a large part of our intuitive category structure, including the global division into animate and inanimate objects, and further hierarchical subdivisions of animate objects. The representation of categories was distributed in several respects, e.g., the similarity of response patterns to stimuli within a category was maintained by both the cells that maximally responded to the category and the cells that responded weakly to the category. These results advance our understanding of the nature of the IT neural code, suggesting an inherently categorical representation that comprises a range of categories including the amply investigated face category.*

Tags: Neuroscience,SDR

[14] Matthew Larkum. A cellular mechanism for cortical associations: an organizing principle for the cerebral cortex. *Trends in neurosciences*, 36(3):141–51, March 2013.

Abstract: *A basic feature of intelligent systems such as the cerebral cortex is the ability to freely associate aspects of perceived experience with an internal representation of the world and make predictions about the future. Here, a hypothesis is presented that the extraordinary performance of the cortex derives from an associative mechanism built in at the cellular level to the basic cortical neuronal unit: the pyramidal cell. The mechanism is robustly triggered by coincident input to opposite poles of the neuron, is exquisitely matched to the large- and fine-scale architecture of the cortex, and is tightly controlled by local microcircuits of inhibitory neurons targeting subcellular compartments. This article explores the experimental evidence and the implications for how the cortex operates.*

[15] Matthew E Larkum, Thomas Nevian, Maya Sandler, Alon Polsky, and Jackie Schiller. Synaptic integration in tuft dendrites of layer 5 pyramidal neurons: a new unifying principle. *Science (New York, N.Y.)*, 325:756–760, 2009.

Abstract: *Tuft dendrites are the main target for feedback inputs innervating neocortical layer 5 pyramidal neurons, but their properties remain obscure. We report the existence of N-methyl-D-aspartate (NMDA) spikes in the fine distal tuft dendrites that otherwise did not support the initiation of calcium spikes. Both direct measurements and computer simulations showed that NMDA spikes are the dominant mechanism by which distal synaptic input leads to firing of the neuron and provide the substrate for complex parallel processing of top-down input arriving at the tuft. These data lead to a new unifying view of integration in pyramidal neurons in which all fine dendrites, basal and tuft, integrate inputs locally through the recruitment of NMDA receptor channels relative to the fixed apical calcium and axosomatic sodium integration points.*

[16] Nuo Li and James J DiCarlo. Unsupervised natural experience rapidly alters invariant object representation in visual cortex. *Science*, 321(5895):1502–1507, 2008.

Abstract: *Object recognition is computationally challenging because each object produces myriad retinal images. Neurons at the highest cortical stage of the primate ventral visual stream (inferior temporal cortex; IT) likely underlie the ability of the visual system to tolerate that image variation – their responses are selective to different objects, yet tolerant (invariant) to changes in object position, scale, pose, etc. (1-6). Understanding object recognition will require solving the mystery of how the brain constructs this neuronal tolerance. Here we report a novel instance of neuronal learning that suggests the underlying solution. Specifically, we*

show that targeted alteration of the natural temporal contiguity of unsupervised visual experience causes specific changes in the position tolerance (invariance) of IT neuronal selectivity. This unsupervised temporal tolerance learning (UTL) is substantial, increases with experience, and is significant even in single IT neurons after just one hour. Coupled with previous theoretical work (7-9) and the finding that this same experience manipulation changes the position tolerance of human object perception (10), we speculate that UTL may reflect the mechanism by which the ventral visual stream builds and maintains tolerant object representations. The relatively fast time-scale and unsupervised nature of UTL open the door to advances in systematically characterizing the spatiotemporal image statistics that drive it, understanding if it plays a role in other types of tolerance, and perhaps connecting a central cognitive ability – tolerant object recognition – to cellular and molecular plasticity mechanisms.

Tags: Neuroscience,Temporal Pooling

[17] Guy Major, Matthew E Larkum, and Jackie Schiller. Active properties of neocortical pyramidal neuron dendrites. *Annual review of neuroscience*, 36:1–24, 2013.

Abstract: *Dendrites are the main recipients of synaptic inputs and are important sites that determine neurons' input-output functions. This review focuses on thin neocortical dendrites, which receive the vast majority of synaptic inputs in cortex but also have specialized electrogenic properties. We present a simplified working-model biophysical scheme of pyramidal neurons that attempts to capture the essence of their dendritic function, including the ability to behave under plausible conditions as dynamic computational subunits. We emphasize the electrogenic capabilities of NMDA receptors (NMDARs) because these transmitter-gated channels seem to provide the major nonlinear depolarizing drive in thin dendrites, even allowing full-blown NMDA spikes. We show how apparent discrepancies in experimental findings can be reconciled and discuss the current status of dendritic spikes in vivo; a dominant NMDAR contribution would indicate that the input-output relations of thin dendrites are dynamically set by network activity and cannot be fully predicted by purely reductionist approaches.*

[18] T. Meyer and C. R. Olson. Statistical learning of visual transitions in monkey inferotemporal cortex, 2011.

Abstract: *One of the most fundamental functions of the brain is to predict upcoming events on the basis of the recent past. A closely related function is to signal when a prediction has been violated. The identity of the brain regions that mediate these functions is not known. We set out to determine whether they are implemented at the level of single neurons in the visual system. We gave monkeys prolonged exposure to pairs of images presented in fixed sequence so that each leading image became a strong predictor for the corresponding trailing image. We then monitored the responses of neurons in the inferotemporal cortex to image sequences that obeyed or violated the transitional rules imposed during training. Inferotemporal neurons exhibited a transitional surprise effect, responding much more strongly to unpredicted transitions than to predicted transitions. Thus, neurons even in the visual system make experience-based predictions and react when they fail.*

Tags: Neuroscience,Sequence Learning

[19] J.-e. K. Miller, I. Ayzenshtat, L. Carrillo-Reid, and R. Yuste. Visual stimuli recruit intrinsically generated cortical ensembles. *Proceedings of the National Academy of Sciences*, 111(38):E4053–61, September 2014.

Abstract: *The cortical microcircuit is built with recurrent excitatory connections, and it has long been suggested that the purpose of this design is to enable intrinsically driven reverberating activity. To understand the dynamics of neocortical intrinsic activity better, we performed two-photon calcium imaging of populations of neurons from the primary visual cortex of awake mice during visual stimulation and spontaneous activity. In both conditions, cortical activity is dominated by coactive groups of neurons, forming ensembles whose activation cannot be explained by the independent firing properties of their contributing neurons, considered in isolation. Moreover, individual neurons flexibly join multiple ensembles, vastly expanding the encoding potential of the circuit. Intriguingly, the same coactive ensembles can repeat spontaneously and in response to visual stimuli, indicating that stimulus-evoked responses arise from activating these intrinsic building blocks. Although the spatial properties of stimulus-driven and spontaneous ensembles are similar, spontaneous ensembles are active at random intervals, whereas visually evoked ensembles are time-locked to stimuli. We conclude that neuronal ensembles, built by the coactivation of flexible groups of neurons, are emergent functional units of cortical activity and propose that visual stimuli recruit intrinsically generated ensembles to represent visual attributes.*

Tags: Neuroscience,SDR,Sequence Learning

[20] Cristopher M Niell, Martin P Meyer, and Stephen J Smith. In vivo imaging of synapse formation on a growing dendritic arbor. *Nature neuroscience*, 7(3):254–60, March 2004.

> **Abstract:** *The form of a neuron's dendritic arbor determines the set of axons with which it may form synaptic contacts, thus establishing connectivity within neural circuits. However, the dynamic relationship between dendrite growth and synaptogenesis is not well understood. To observe both processes simultaneously, we performed long-term imaging of non-spiny dendritic arbors expressing a fluorescent postsynaptic marker protein as they arborized within the optic tectum of live zebrafish larvae. Our results indicate that almost all synapses form initially on newly extended dendritic filopodia. A fraction of these nascent synapses are maintained, which in turn stabilizes the subset of filopodia on which they form. Stabilized filopodia mature into dendritic branches, and successive iterations of this process result in growth and branching of the arbor. These findings support a 'synaptotropic model' in which synapse formation can direct dendrite arborization.*

> **Tags:** Synapses

[21] B A Olshausen and D J Field. Emergence of simple-cell receptive field properties by learning a sparse code for natural images. *Nature*, 381(6583):607–9, June 1996.

> **Abstract:** *The receptive fields of simple cells in mammalian primary visual cortex can be characterized as being spatially localized, oriented and bandpass (selective to structure at different spatial scales), comparable to the basis functions of wavelet transforms. One approach to understanding such response properties of visual neurons has been to consider their relationship to the statistical structure of natural images in terms of efficient coding. Along these lines, a number of studies have attempted to train unsupervised learning algorithms on natural images in the hope of developing receptive fields with similar properties, but none has succeeded in producing a full set that spans the image space and contains all three of the above properties. Here we investigate the proposal that a coding strategy that maximizes sparseness is sufficient to account for these properties. We show that a learning algorithm that attempts to find sparse linear codes for natural scenes will develop a complete family of localized, oriented, bandpass receptive fields, similar to those found in the primary visual cortex. The resulting sparse image code provides a more efficient representation for later stages of processing because it possesses a higher degree of statistical independence among its outputs.*

> **Tags:** SDR

[22] Bruno A. Olshausen and David J. Field. Sparse coding with an overcomplete basis set: A strategy employed by V1? *Vision Research*, 37:3311–3325, 1997.

> **Abstract:** *The spatial receptive fields of simple cells in mammalian striate cortex have been reasonably well described physiologically and can be characterized as being localized, oriented, and bandpass, comparable with the basis functions of wavelet transforms. Previously, we have shown that these receptive field properties may be accounted for in terms of a strategy for producing a sparse distribution of output activity in response to natural images. Here, in addition to describing this work in a more expansive fashion, we examine the neurobiological implications of sparse coding. Of particular interest is the case when the code is overcomplete - i.e., when the number of code elements is greater than the effective dimensionality of the input space. Because the basis functions are non-orthogonal and not linearly independent of each other, sparsifying the code will recruit only those basis functions necessary for representing a given input, and so the input-output function will deviate from being purely linear. These deviations from linearity provide a potential explanation for the weak forms of non-linearity observed in the response properties of cortical simple cells, and they further make predictions about the expected interactions among units in response to naturalistic stimuli.*

> **Tags:** SDR

[23] Bruno A. Olshausen and David J. Field. Sparse coding of sensory inputs, 2004.

> **Abstract:** *Several theoretical, computational, and experimental studies suggest that neurons encode sensory information using a small number of active neurons at any given point in time. This strategy, referred to as 'sparse coding', could possibly confer several advantages. First, it allows for increased storage capacity in associative memories; second, it makes the structure in natural signals explicit; third, it represents complex data in a way that is easier to read out at subsequent levels of processing; and fourth, it saves energy. Recent physiological recordings from sensory neurons have indicated that sparse coding could be a ubiquitous strategy employed in several different modalities across different organisms. ?? 2004 Elsevier Ltd. All rights reserved.*

> **Tags:** SDR

[24] Lucy M Palmer, Adam S Shai, James E Reeve, Harry L Anderson, Ole Paulsen, and Matthew E Larkum. NMDA spikes enhance action potential generation during sensory input. *Nature neuroscience*, 17:383–90, 2014.

> **Abstract:** *Recent evidence in vitro suggests that the tuft dendrites of pyramidal neurons are capable of evoking local NMDA receptor-dependent electrogenesis, so-called NMDA spikes. However, it has so far proved difficult to demonstrate their existence in vivo. Moreover, it is not clear whether NMDA spikes are relevant to the output of pyramidal neurons. We found that local NMDA spikes occurred in tuft dendrites of layer 2/3 pyramidal neurons both spontaneously and following sensory input, and had a large influence on the number of output action potentials. Using two-photon activation of an intracellular caged NMDA receptor antagonist (tc-MK801), we found that isolated NMDA spikes typically occurred in multiple branches simultaneously and that sensory stimulation substantially increased their probability. Our results demonstrate that NMDA receptors have a vital role in coupling the tuft region of the layer 2/3 pyramidal neuron to the cell body, enhancing the effectiveness of layer 1 input.*

> **Tags:** Dendrites,Neuroscience

[25] Gerard J. Rinkus. Sparsey: event recognition via deep hierarchical sparse distributed codes. *Frontiers in Computational Neuroscience*, 8, December 2014.

> **Abstract:** *The visual cortexs hierarchical, multi-level organization is captured in many biologically inspired computational vision models, the general idea being that progressively larger scale (spatially/temporally) and more complex visual features are represented in progressively higher areas. However, most earlier models use localist representations (codes) in each representational field (which we equate with the cortical macrocolumn, mac), at each level. In localism, each represented feature/concept/event (hereinafter item) is coded by a single unit. The model we describe, Sparsey, is hierarchical as well but crucially, it uses sparse distributed coding (SDC) in every mac in all levels. In SDC, each represented item is coded by a small subset of the macs units. The SDCs of different items can overlap and the size of overlap between items can be used to represent their similarity. The difference between localism and SDC is crucial because SDC allows the two essential operations of associative memory, storing a new item and retrieving the best-matching stored item, to be done in fixed time for the life of the model. Since the models core algorithm, which does both storage and retrieval (inference), makes a single pass over all macs on each time step, the overall models storage/retrieval operation is also fixed-time, a criterion we consider essential for scalability to the huge (Big Data) problems. A 2010 paper described a non-hierarchical version of this model in the context of purely spatial pattern processing. Here, we elaborate a fully hierarchical model (arbitrary numbers of levels and macs per level), describing novel model principles like progressive critical periods, dynamic modulation of principal cells activation functions based on a mac-level familiarity measure, representation of multiple simultaneously active hypotheses, a novel method of time warp invariant recognition, and we report results showing learning/recognition of spatiotemporal patterns.*

[26] S. Murray Sherman and Rainer W. Guillery. *Functional Connections of Cortical Areas: A New View from the Thalamus*. The MIT Press, 2013.

> **Abstract:** *In this book, two leading authorities on the thalamus and its relationship to cortex build on their earlier findings to arrive at new ways of thinking about how the brain relates to the world, to cognition, and behavior. Based on foundations established earlier in their book Exploring the Thalamus and Its Role in Cortical Function, the authors consider the implications of these ground rules for thalamic inputs, thalamocortical connections, and cortical outputs. The authors argue that functional and structural analyses of pathways connecting thalamus and cortex point beyond these to lower centers and through them to the body and the world. Each cortical area depends on the messages linking it to body and world. These messages relate to the way we act and think; each cortical area receives thalamic inputs and has outputs to motor centers. Sherman and Guillery go on to discuss such topics as the role of branching axons that carry motor instructions as well as copies of these motor instructions for relay to cortex under the control of the thalamic gate. This gate allows the thalamus to control the passage of information on the basis of which cortex relates to the rest of the nervous system.*

> **Tags:** Neuroscience,Thalamus

[27] Marc A Sommer and Robert H Wurtz. Influence of the thalamus on spatial visual processing in frontal cortex. *Nature*, 444(7117):374–7, November 2006.

> **Abstract:** *Each of our movements activates our own sensory receptors, and therefore keeping track of self-movement is a necessary part of analysing sensory input. One way in which the*

brain keeps track of self-movement is by monitoring an internal copy, or corollary discharge, of motor commands. This concept could explain why we perceive a stable visual world despite our frequent quick, or saccadic, eye movements: corollary discharge about each saccade would permit the visual system to ignore saccade-induced visual changes. The critical missing link has been the connection between corollary discharge and visual processing. Here we show that such a link is formed by a corollary discharge from the thalamus that targets the frontal cortex. In the thalamus, neurons in the mediodorsal nucleus relay a corollary discharge of saccades from the midbrain superior colliculus to the cortical frontal eye field. In the frontal eye field, neurons use corollary discharge to shift their visual receptive fields spatially before saccades. We tested the hypothesis that these two components-a pathway for corollary discharge and neurons with shifting receptive fields-form a circuit in which the corollary discharge drives the shift. First we showed that the known spatial and temporal properties of the corollary discharge predict the dynamic changes in spatial visual processing of cortical neurons when saccades are made. Then we moved from this correlation to causation by isolating single cortical neurons and showing that their spatial visual processing is impaired when corollary discharge from the thalamus is interrupted. Thus the visual processing of frontal neurons is spatiotemporally matched with, and functionally dependent on, corollary discharge input from the thalamus. These experiments establish the first link between corollary discharge and visual processing, delineate a brain circuit that is well suited for mediating visual stability, and provide a framework for studying corollary discharge in other sensory systems.

Tags: Sensorimotor Inference

[28] Nelson Spruston. Pyramidal neurons: dendritic structure and synaptic integration. *Nature reviews. Neuroscience*, 9(3):206–21, March 2008.

Abstract: *Pyramidal neurons are characterized by their distinct apical and basal dendritic trees and the pyramidal shape of their soma. They are found in several regions of the CNS and, although the reasons for their abundance remain unclear, functional studies–especially of CA1 hippocampal and layer V neocortical pyramidal neurons–have offered insights into the functions of their unique cellular architecture. Pyramidal neurons are not all identical, but some shared functional principles can be identified. In particular, the existence of dendritic domains with distinct synaptic inputs, excitability, modulation and plasticity appears to be a common feature that allows synapses throughout the dendritic tree to contribute to action-potential generation. These properties support a variety of coincidence-detection mechanisms, which are likely to be crucial for synaptic integration and plasticity.*

Tags: Pyramidal neurons

[29] Alex M Thomson. Neocortical layer 6, a review. *Frontiers in neuroanatomy*, 4:13, 2010.

Abstract: *This review attempts to summarise some of the major areas of neocortical research as it pertains to neocortical layer 6. After a brief summary of the development of this intriguing layer, the major pyramidal cell classes to be found in layer 6 are described and compared. The connections made and received by these different classes of neurones are then discussed and the possible functions of these connections, with particular reference to the shaping of responses in visual cortex and thalamus. Inhibition in layer 6 is discussed where appropriate, but not in great detail. Many types of interneurones are to be found in each cortical layer and layer 6 is no exception, but the functions of each type remain to be elucidated (Gonchar et al., 2007).*

Tags: Anatomy,Neuroscience

[30] Alex M Thomson and a Peter Bannister. Interlaminar connections in the neocortex. *Cerebral cortex (New York, N.Y. : 1991)*, 13(1):5–14, January 2003.

Abstract: *This review summarizes the local circuit, interlaminar connections in adult mammalian neocortex. These were first demonstrated with anatomical techniques, which indicate some of the exquisite spatial precision present in the circuitry. Details, such as the class(es) of neurons targeted by some of these projections, have begun to be added in studies that combine paired/triple intracellular recordings with dye-filling of connected neurons. Clear patterns are emerging from these studies, with 'forward' projections from layer 4 to 3 and from 3 to 5 targeting both selected pyramidal cells and interneurons, while 'back' projections from layer 5 to 3 and from 3 to 4 target only interneurons. To place these data in a wider context, the major afferent inputs to and efferent outputs from each of the layers are discussed first.*

Tags: Anatomy,Laminar structure,Neuroscience

[31] Alex M Thomson and Christophe Lamy. Functional maps of neocortical local circuitry. *Frontiers in neuroscience*, 1:19–42, 2007.

Abstract: *This review aims to summarize data obtained with different techniques to provide a functional map of the local circuit connections made by neocortical neurones, a reference for those interested in cortical circuitry and the numerical information required by those wishing to model the circuit. A brief description of the main techniques used to study circuitry is followed by outline descriptions of the major classes of neocortical excitatory and inhibitory neurones and the connections that each layer makes with other cortical and subcortical regions. Maps summarizing the projection patterns of each class of neurone within the local circuit and tables of the properties of these local circuit connections are provided.This review relies primarily on anatomical studies that have identified the classes of neurones and their local and long distance connections and on paired intracellular and whole-cell recordings which have documented the properties of the connections between them. A large number of different types of synaptic connections have been described, but for some there are only a few published examples and for others the details that can only be obtained with paired recordings and dye-filling are lacking. A further complication is provided by the range of species, technical approaches and age groups used in these studies. Wherever possible the range of available data are summarised and compared. To fill some of the more obvious gaps for the less well-documented cases, data obtained with other methods are also summarized.*

Tags: Anatomy,Neuroscience

[32] Joshua T Trachtenberg, Brian E Chen, Graham W Knott, Guoping Feng, Joshua R Sanes, Egbert Welker, and Karel Svoboda. Long-term in vivo imaging of experience-dependent synaptic plasticity in adult cortex. *Nature*, 420(6917):788–94, 2002.

Abstract: *Do new synapses form in the adult cortex to support experience-dependent plasticity? To address this question, we repeatedly imaged individual pyramidal neurons in the mouse barrel cortex over periods of weeks. We found that, although dendritic structure is stable, some spines appear and disappear. Spine lifetimes vary greatly: stable spines, about 50% of the population, persist for at least a month, whereas the remainder are present for a few days or less. Serial-section electron microscopy of imaged dendritic segments revealed retrospectively that spine sprouting and retraction are associated with synapse formation and elimination. Experience-dependent plasticity of cortical receptive fields was accompanied by increased synapse turnover. Our measurements suggest that sensory experience drives the formation and elimination of synapses and that these changes might underlie adaptive remodelling of neural circuits.*

Tags: Synapses

[33] William E. Vinje and Jack L. Gallant. Natural Stimulation of the Nonclassical Receptive Field Increases Information Transmission Efficiency in V1. *J. Neurosci.*, 22(7):2904–2915, April 2002.

Abstract: *We have investigated how the nonclassical receptive field (nCRF) affects information transmission by V1 neurons during simulated natural vision in awake, behaving macaques. Stimuli were centered over the classical receptive field (CRF) and stimulus size was varied from one to four times the diameter of the CRF. Stimulus movies reproduced the spatial and temporal stimulus dynamics of natural vision while maintaining constant CRF stimulation across all sizes. In individual neurons, stimulation of the nCRF significantly increases the information rate, the information per spike, and the efficiency of information transmission. Furthermore, the population averages of these quantities also increase significantly with nCRF stimulation. These data demonstrate that the nCRF increases the sparseness of the stimulus representation in V1, suggesting that the nCRF tunes V1 neurons to match the highly informative components of the natural world.*

Tags: Neuroscience,Sequence Learning

[34] John T Wixted, Larry R Squire, Yoonhee Jang, Megan H Papesh, Stephen D Goldinger, Joel R Kuhn, Kris A Smith, David M Treiman, and Peter N Steinmetz. Sparse and distributed coding of episodic memory in neurons of the human hippocampus. *Proceedings of the National Academy of Sciences of the United States of America*, 111(26):9621–6, July 2014.

Abstract: *Neurocomputational models hold that sparse distributed coding is the most efficient way for hippocampal neurons to encode episodic memories rapidly. We investigated the representation of episodic memory in hippocampal neurons of nine epilepsy patients undergoing intracranial monitoring as they discriminated between recently studied words (targets) and new words (foils) on a recognition test. On average, single units and multiunits exhibited higher spike counts in response to targets relative to foils, and the size of this effect correlated with behavioral performance. Further analyses of the spike-count distributions revealed*

that (i) a small percentage of recorded neurons responded to any one target and (ii) a small percentage of targets elicited a strong response in any one neuron. These findings are consistent with the idea that in the human hippocampus episodic memory is supported by a sparse distributed neural code.

Tags: SDR

[35] D M. Wolpert and R C. Miall. Forward Models for Physiological Motor Control. *Neural networks : the official journal of the International Neural Network Society*, 9(8):1265–1279, November 1996.

Abstract: *Based on theoretical and computational studies it has been suggested that the central nervous system (CNS) internally simulates the behaviour of the motor system in planning, control and learning. Such an internal "forward" model is a representation of the motor system that uses the current state of the motor system and motor command to predict the next state. We will outline the uses of such internal models for solving several fundamental computational problems in motor control and then review the evidence for their existence and use by the CNS. Finally we speculate how the location of an internal model within the CNS may be identified. Copyright 1996 Elsevier Science Ltd.*

[36] Guang Yang, Cora Sau Wan Lai, Joseph Cichon, Lei Ma, Wei Li, and Wen-Biao Gan. Sleep promotes branch-specific formation of dendritic spines after learning. *Science (New York, N.Y.)*, 344(6188):1173–8, June 2014.

Abstract: *How sleep helps learning and memory remains unknown. We report in mouse motor cortex that sleep after motor learning promotes the formation of postsynaptic dendritic spines on a subset of branches of individual layer V pyramidal neurons. New spines are formed on different sets of dendritic branches in response to different learning tasks and are protected from being eliminated when multiple tasks are learned. Neurons activated during learning of a motor task are reactivated during subsequent non-rapid eye movement sleep, and disrupting this neuronal reactivation prevents branch-specific spine formation. These findings indicate that sleep has a key role in promoting learning-dependent synapse formation and maintenance on selected dendritic branches, which contribute to memory storage.*

Tags: Dendrites,Sequence Learning

[37] Karen Zito and Karel Svoboda. Activity-dependent synaptogenesis in the adult Mammalian cortex. *Neuron*, 35(6):1015–7, September 2002.

Abstract: *Recent electron microscopic studies provide evidence that the adult cortex generates new synapses in response to sensory activity and that these structural changes can occur rapidly, within 24 hr of sensory stimulation. Together with progress imaging synapses in vivo, the stage appears set for advances in understanding the dynamics and mechanisms of experience-dependent synaptogenesis.*

Tags: Synapses