

# Dendritic+ Processing in an Emergic Network Model of Narrow Slit Viewing

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## Abstract

Accounting for dendritic+ processing facilitates richer neural encoding schemes that can ultimately lead to simpler networks while improving their neurobiological plausibility. Dendritic+ processing is an example of several modeling tradeoffs: how local complexifications can improve global simplicity, and how functional *network circuitry* can be traded against *representational circuitry*. This is demonstrated within a model of narrow slit viewing based on an emergic network architecture (Leibovitz & West, 2012).

**Keywords:** Dendritic processing; Emergic Cognitive Model (ECM); Emergic Network (EN); Flowcentric; Neural coding; Representation; Slit Viewing; Unified Modeling.

## Introduction

Each type of artificial neural network is an idealization that simplifies neurophysiology for a specific epistemic purpose. There are numerous different types of networks, each with its own way of approximating the behavior of actual neurons. For example, most systems treat connections between units in a generic fashion assuming a *single value* is transmitted and requiring at most a weighting factor and perhaps a temporal delay to differentiate one connection from another. Each connection can be thought of as a prototypical chemical synapse as shown in the left half of Figure 1. Dendritic processing, if any, can be ignored as it is subsumed by the synaptic abstraction. The artificial unit, therefore, can be thought of as computing a *single activation function* over a weighted sum of equipotent inputs (Cazé, Humphries, & Gutkin, 2013). This drives the *simple* and *single* valued output directly, or updates an internal state in dynamic models.

We classify as *dendritic+* as those cases where a unit is considered to compute more than one ‘function’, i.e., where connections cannot be treated homogeneously and may have different purposes, where multiple outputs are computed, or where encoded values are structured and may vary. Typically, interactions between signals occur. This is often realized via multiple non-linear compartments within dendrites (London & Häusser, 2005), but other physiological forms beyond dendrites can also be responsible (hence the + suffix). As one example, “a single A17 [amacrine interneuron] contains, on average, more than 100 independent input/output microcircuits operating in parallel” (Grimes, Zhang, Graydon, Kachar, & Diamond, 2010). But do such local details matter to higher levels of analysis? Explorations involving *emergic networks* (Leibovitz, 2013) suggest that they do. Our hypotheses and initial results are presented here.

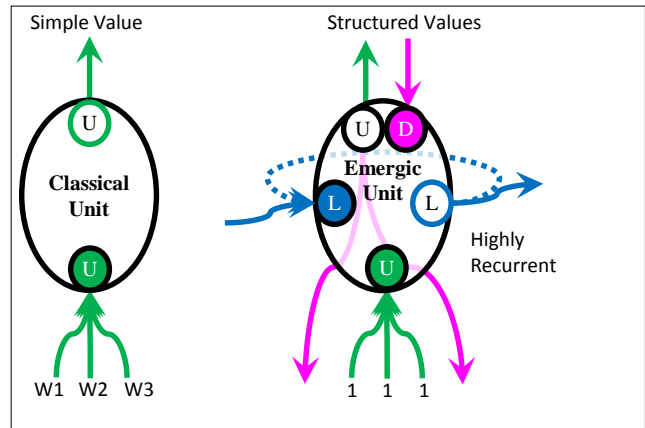


Figure 1: Single feedforward (**Up**) flow in a prototypical classical unit vs. multiple interacting (**Up, Down & Lateral**) flows of a prototypical Emergic unit.

Contrasted to classical units, emergic units have *multiple* output flows (and different kinds of input flows) and use *emergic ports* to functionally segregate associated inputs and outputs (right half of Figure 1), and to support varying encoding schemes. Emergic *links* between units typically do not use weights and typically have a common temporal delay of at least one *tick* – nominally 10ms. So although emergic networks are more abstract than spiking neural networks in terms of individual spike details, they are more comprehensive in terms of informational interactions that can implicate finer-grained dendritic processes. Each emergic unit computes the interaction of flows (see Larkum, Nevian, Sandler, Polsky, & Schiller, 2009) which can be considered as a function for each output. These aforementioned difference do not in themselves mandate special dendritic processing. However, the values transmitted between emergic units can be highly structured therefore the decoding and interactions of structural items can account for dendritic processing.

## Narrow Slit Viewing

A model of narrow slit viewing (Leibovitz, 2013) makes use of receptive field (RF) units as illustrated in Figure 2. In particular, to support the integration of narrow slit views onto the wider anorthoscopic sensation required tagging visual

content, i.e., the amount of blue colour sensed by an S cone, with its spatial extent. Thus, emergic values that constitute the flow of visual information are structured and effectively spatiotopic. RFs remap their views to compensate for eye motion (Merriam, Genovese, & Colby, 2007), and the emergic input ports are responsible for picking out and summing the portion of surrounding emergic values *in the flow* that overlap with their unit's new position. It is the handling of space under motion that leads to significant interaction within the locus of each RF (and each input port) as indicated by the intra-unit red coloured flows of Figure 2, and it is this behaviour that implicates dendritic processes.

### Flowcentric Model Behaviour

The complexifications exemplified by Figure 2 can be understood in relation to the narrow slit phenomenology demonstrated by the model. Anorthoscopic perception is perception under abnormal viewing conditions. One such scenario is when a *wider* view of the world is *perceived* than can be *sensed* through a *narrow* slit. The narrow view of the model is shown in Figure 3. The retina moved back and forth across a wider stimulus (Figure 4) while blinking occurred. Figure 5 shows the wider sensation when the eye was at its rightmost position and the flowcentric memory appears on the left within the neural mosaic. Figure 6 shows the wider sensation when the eye was at its leftmost position and the flowcentric memory appears on the right within the neural mosaic. For the purposes of this paper, the entire behaviour of the model can be explained by a single class of neural units making up the mosaic – the Receptive Fields (RFs) units of Figure 2 arranged with lateral connectivity into a heterogeneous mosaic. Animated results are available at <http://dpleibovitz.upwize.com/?p=373>.

### Computational Model

An Emergic Cognitive Model (ECM) for low level vision (Leibovitz, 2013) is shown in Figure 7 and was customized to demonstrate the narrow slit phenomenology. The ECM, in turn, is based on the Emergic Network (EN) architecture (Leibovitz & West, 2012). Both inform our discussion. For example, Figure 2 defines the RF unit that compromises the RF hierarchy within ECM. The EN defines the abilities of units and ports generically and suggests a distinction between unit computations supporting network functions and port computations supporting functional representations. One way to understand this is as a tradeoff in network vs. dendritic circuitry.

### Emergic Cognitive Model (ECM)

The ECM is primarily based on a single Receptive Field (RF) unit that is the locus of two functions as illustrated in Figure 2. The RFs are arranged in a horizontal mosaic (shown in Figure 5, and Figure 6) having lateral connectivity and are also arranged vertically into a spatiotemporal hierarchy with additional bottom-up and top-down connectivity (Figure 7). The vertical hierarchy is mostly ignored within this paper, as are the segmentation *layers*. During a blink, information does

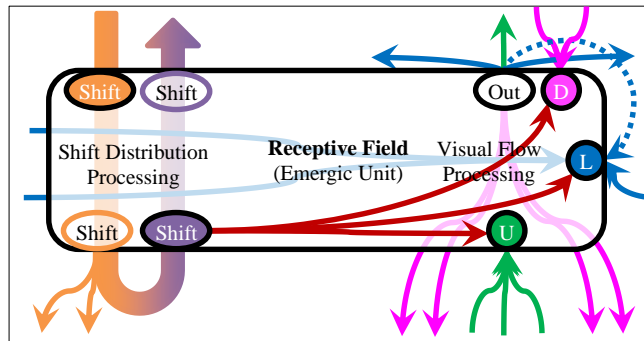


Figure 2: Functional interactions in an actual Emergic RF

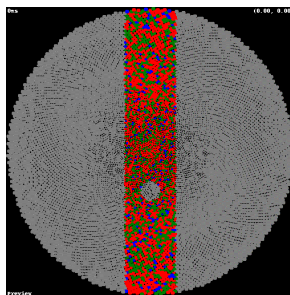


Figure 3: Narrow Retina

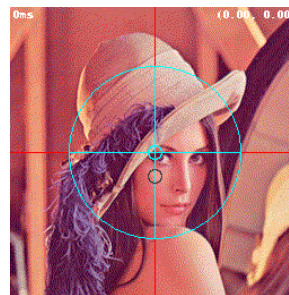


Figure 4: Wide Stimulus

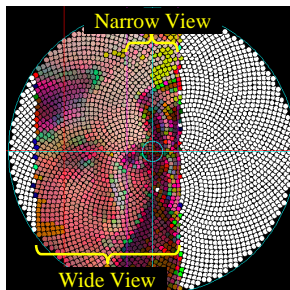


Figure 5: Anorthoscopic Sensation @ 140ms

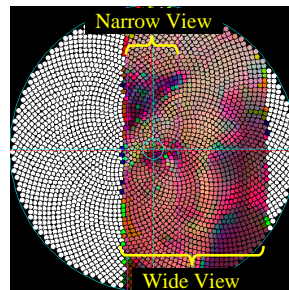


Figure 6: Anorthoscopic Sensation @ 220ms

not flow upwards from the photoreceptors, so lateral RF connectivity effects a flowcentric form of memory-in-motion. Under motion, this can also fill-in the blind-spot and fill-out the wider anorthoscopic view.

### Functional Pathways/Streams/Flows

The ECM has two main pathways, streams or flows that correspond roughly to the vision for perception and action distinction (Goodale & Milner, 1992). These are depicted on the left or right half portions of the RF shown within Figure 2. However, for this paper we will focus on the interactions between these pathways.

#### Visual Content on Right Hand Side of RF

The visual stimuli is processed on the right hand side (RHS) within each RF. Here, bottom-up, top-down and lateral flows of visual information interact according to the *handling missing data* function that supports temporal and spatial forms of completion (Leibovitz & West, 2013). Lateral flows

effect the temporal form of completion – an instantaneous *cut & paste* from the previous frame (Van Roosmalen, Kokaram, & Biemond, 1999). Top-down flows effect the slower spatial form of completion. In either form, completion respects borders but without explicit border processing. This is due to the nature of calculating the spatial extent of visual information via dendritic processing and will be further detailed.

### Shift Content on Left Hand Side of RF

On the left hand side (LHS) within each RF, motion compensation or shift information for advanced eye motor plans is distributed down the RF hierarchy and reflected back up as part of the *maintaining information coherence* function. This is arranged such that as visual information flows upwards, it is synchronised with motor plans. The RHS input ports named **U**, **D** and **L** only accept visual values tagged with the correctly shifted spatiotopic coordinates via dendritic processing to be further detailed. In this way, the two functions interact within the locus of every RF.

Although the LHS is represented within the RF as four ports, its neurobiological foundation and encoding is completely different. The distribution of advanced motor plans is via the corollary discharge (or efference copy) of intended eye motor commands (Hall & Colby, 2011). While this starts off at a high level with dedicated neural circuitry (Shin & Sommer, 2012), by the time it reaches the RFs, we hypothesize that it is likely manifest as travelling waves (see Sato, Nauhaus, & Carandini, 2012) or variations in the local field potential (LFP) corresponding to synchronized/coherent neural activity (Harris & Thiele, 2011). Therefore, it would only be the dendrites on the RHS which will be sensitive to these LFP variations.

### Structured Emergic Values

Emergic values can be highly structured to encode multiple items simultaneously. The ECM encodes descriptive statistics to represent the underlying spike distribution, as well as the spatial extent of colour values (also in statistical form).

### Descriptive Statistics

The emergic *values* that flow between emergic *units* across emergic *links* can be highly structured. Every neuron, or pool of neurons, generates information (spikes) whose distribution can be statistically *described*. For example, a given rate encoding will have an average rate over a long period that varies over smaller periods. This variance need not be informative nor functional. However, because we wish to place an RF within a spatiotemporal hierarchy (Figure 7), it would be expedient if our statistical representation supports spatiotemporal summation naturally. Population sampling statistics represented in the following *incremental* form within an emergic value will do the trick. Let  $v$  be the simple real value encoded by classical frameworks. Then an emergic value need only maintain:

- n: the number of values sampled =  $\sum 1$
- sv: sum of values =  $\sum v_n$
- svv: sum of values squared =  $\sum v_n^2$

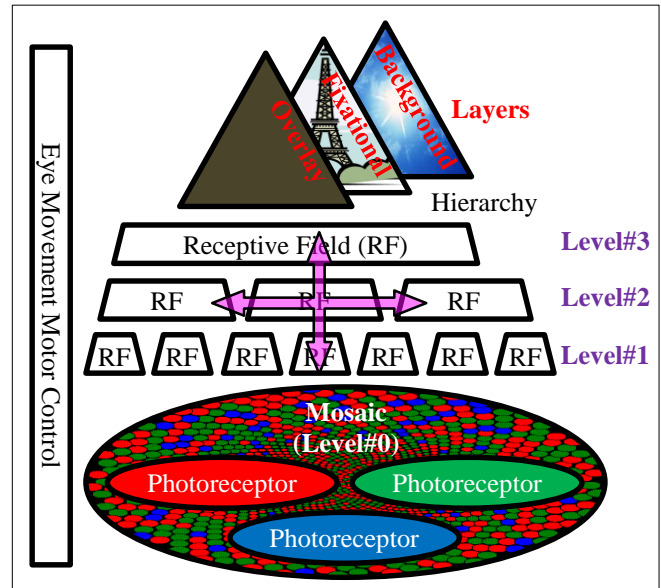


Figure 7: ECM Structural Summary

The above computations are performed incrementally within *summing* input ports as emergic values arrive (in an arbitrary order). This provides sufficient information to calculate

$$\begin{aligned} \text{mean}(v): & \quad sv/n \\ \text{variance}(v): & \quad (svv - sv^2/n)/n \\ \text{sd}(v): & \quad \sqrt{\text{variance}} \end{aligned}$$

for any RF at any level in the hierarchy. On the other hand, the ‘shift’ ports of Figure 2 have single inputs and do not require summation. Indeed, they have their own dedicated encodings for signaling planned eye movements.

### Biological Plausibility of Descriptive Statistics

One functional role of such statistics is a decrease in variance and an increase in accuracy over larger sample populations, i.e., as one goes up the RF hierarchy. This is supported by the phenomenon of visual hyperacuity where vernier accuracy is typically 1/6<sup>th</sup> the size of the smallest foveal cone and suggests some form of integrating information among neighboring RFs (Wilson, 1986). Because vernier accuracy is still good over blind spots (Crossland & Bex, 2009) this lends further support to our flowcentric model where vernier stimuli can flow over blind spots and still be integrated. Similarly, at a neurobiological level, it was found that CA1 place fields within the hippocampus are *sharpened* by synchronous inputs of overlapping entorhinal (EC) and CA3 cells (Ahmed & Mehta, 2009). In many cases, the temporal variance or irregularity *is* the neural code (Van Hemmen & Sejnowski, 2006), so encoding it explicitly matches biology.



Thus we take this as supporting our view that descriptive statistics are more than mere *descriptions* but encapsulate actual cognitive *mechanisms*.

### Tagging Colour with Spatial Extent for Summation

Every visual value, i.e., the amount of blue colour sensed by an S cone, is tagged by its spatial extent in the horizontal (x) and vertical (y) dimensions. We use the same descriptive mechanism as for  $v$ . Let  $x$  and  $y$  be simple real values representing the *spatiotopic* center of the photoreceptor ( $\pm$  its radius), then an emergic value contains these additional components

$$\begin{array}{l|l} \text{sx: } \sum x_n & \text{sy: } \sum y_n \\ \text{sxx: } \sum x_n^2 & \text{syy: } \sum y_n^2 \end{array}$$

and provides

$$\text{sd}(x): \sqrt{(\text{sxx} - \text{sx}^2/n)/n} \quad | \quad \text{sd}(y): \sqrt{(\text{syy} - \text{sy}^2/n)/n}$$

Note that because eye movement is planned in advanced and distributed to all RFs, transforming their physical retinotopic coordinates to dynamic spatiotopic coordinates is simply a matter of adding the distributed shifts. We use the *standard deviation* of a value's (x,y) position to define its spatial extent "in the flow." The emergic ports sum up the spatiotopic values based on the percentage overlap with their own physical spatiotopic extents.

Let us now assume that the eye is currently experiencing a blink while moving. Each RF can ensure its colour value is remembered by broadcasting its output laterally within a local fan-out – the lateral "flow". If the eye has moved by three RF position rightwards, than the RF three places to the left would accept that old value and simply rebroadcast it into the flow to be remembered for the next tick. In this way, values can be said to flow over the RFs. If the lateral fan-out was 7 RFs wide, than a value could flow as far as 35 RFs in 5 steps.

If RFs were arranged rectilinearly, then there would be no loss of information and unit behaviour could be described as operating much like a perfect *shift register* (despite broadcasting a value much like over a LAN). However, neurons are neither heterogeneous in location nor size. A perfect shift for RF<sub>1</sub> would be imperfect for other RFs. Therefore the output colour value from RF<sub>2</sub> would likely need to be split across the two or three destination RFs that it now overlaps. They would only accept their portion of the colour value based on the percentage of overlap. Similarly, RF<sub>2</sub> would need to join and sum colour values coming from the two or three lateral RFs that now overlap its own updated spatiotopic position. This constant splitting and merging of colour information leads to a memory that slowly dissipates towards the global average as can be seen in the oldest portion of the flowcentric memories within Figure 5 and Figure 6 – those furthest away from the narrow view.

The merging and splitting of old values is visualized in Figure 8. RFs are "squared" for convenience, and in this example, the yellow, red, green and blue areas represent RF values sent out from the old RF position, and the transparent white overlays represent these same RFs shifted to the right by ½ an RF width. Thus the leftmost RF which had output yellow onto the flow, will merge ½ its old value, with ¼ of

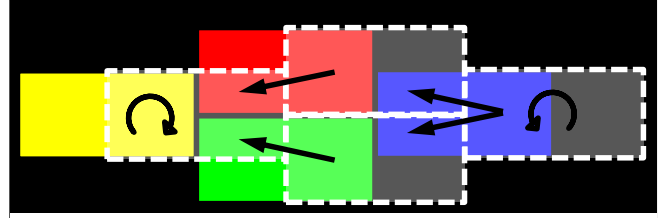


Figure 8: Merging & splitting colour values after a shift

the red and ¼ of the green values from the lateral flow producing a lighter yellow that it will retransmit back into the flow. The RF on the right demonstrates that its old blue value is split ¼ to the middle-top RF and ¼ to the middle-bottom RF (and ½ back to itself).

### Biological Plausibility of Spatial Tagging

Corollary discharge (CD) is a ubiquitous phenomenon throughout the sensory systems (Hall & Colby, 2011) and encodes (somehow) intended motor plans or *shifts*. In the ECM model, shift information could be delivered to the neurons over a connections from a dedicated CD network but this would require adding such a network to the model. Using dendritic+ processing provides a more efficient solution. Shift information can be multiplexed on top of the existing colour value signal by modulating other properties such as amplitude or phase. For example hippocampal CA1 pyramidal neurons can convey spatiotemporal information by modulating their firing patterns from regular to bursting and this is accomplished via dendritic processes (Pissadaki, Sidiropoulou, Reczko, & Poirazi, 2010). Mice whiskers multiplex vertical, horizontal and radial coordinates via the line code, activation timing and activation intensity respectively (Knutsen & Ahissar, 2009), and it is the nonlinear dendritic processes that integrate such information with active sensing behaviour (Xu et al., 2012).

While receptive fields are known to remap, the supposed mechanism is via "tuning" (Burr & Morrone, 2012) although it is not apparent what is being tuned. The word *tune* is simply a surrogate for the word *remap*. Instead, we hypothesize that the CD signal manifests as modulations in the local field potential (LFP), possibly via gamma band neural phase synchrony (Chen et al., 2011). This would result in traveling/propagating waves that would be distributed to all ports (dendrites) so that they could perform summation taking percentage of overlap into account. This would still lead to remapping behaviour. Gamma band oscillations play an intrinsic role in updating representations of visual space (Forgacs et al., 2004). See also (Melloni, Schwiedrzik, Rodriguez, & Singer, 2009).

Indeed, we do not think that a shift amount is explicitly encoded as suggested by the ECM approximation, but that it is a relative code due to phase differences between colour value signals and LFP modulations, a form of ephaptic coupling (Anastassiou, Perin, Markram, & Koch, 2011). For example, Ito et al. (2011) found that under free viewing conditions, LFP oscillations in the alpha-beta band are locked to the onset of a saccade, as is the low-gamma power (Ito,

Maldonado, & Grün, 2013). This can serve as a reference clock to temporal (phase) information within neural spikes. For example, the theta phase can encode two dimensions (trajectory & heading) in the rat hippocampus (Huxter, Senior, Allen, & Csicsvari, 2008), and in further neural regions (Malhotra, Cross, & Van der Meer, 2012). Propagating waves organize spatial phase distributions (Wu, Xiaoying Huang, & Chuan Zhang, 2008).

In general, temporal codes based on both rate and phase can carry significant amounts of extra information. In Layer 4 of the cat's primary visual cortex up to 90% of the extra information can be carried (Basalyga, Montemurro, & Wennekers, 2013).

Finally, the dendritic work within the ports is to perform summation taking the amount of overlap into account. This is effectively a temporal filter (George, Lyons-Warren, Ma, & Carlson, 2011) between LFP phase indicating RF position (as the wave propagates across RF mosaic), and signal phase indicating colour value extent. The closer the phases, the stronger the overlap – a form of dendritic coincidence detection (Jaslove, 1992; Spruston, 2008).

## Discussion

Emergic networks permit the interactions of multiple encoded flows of information. In order to *maintain information coherence* under continuous motion, neurons must remap their receptive fields to compensate for eye motion. This plausibly requires a corollary discharge signal to encode intended eye movement so that it can be distributed to all RFs in time. While the ECM models this via generic links, it must be understood as modifying the local field potential (LFP) which is further distributed to the input ports. These perform spatiotemporal summation via dendritic processes that take the overlap between the RF's new position and the spatial extent of the colour values into account. The values have been broadcast into the flow over a local fan-out, but only accepted at the correct location giving the appearance of a lossy shift register that suffers dissipation.

Leibovitz & West (2013) have shown that because values are encoded with spatial extent, this allows interpolation between two RFs but not extrapolation beyond the extent of an RF (Figure 9). Effectively this causes completion effects to emerge that respect borders, but without explicit border processing. Thus only a single computational unit (the RF) is required. This can be contrasted with the many unit types and parameters of FACADE based models (e.g., Grossberg & Rudd, 1992). In FACADE network level circuitry is required to explicitly handle borders, surface features, and borders under motion. Our network circuitry is simplified by complexifications at the dendritic level that handle the representation of colour values along with their spatial extent in ECM.

Thus ECM demonstrates that when all functional flows are explicated in a model, they may suggest specific encoding schemes that may implicated dendritic processes. ECM is thus more complicated in some respects – within the local aspect of a unit, but the global network level is greatly

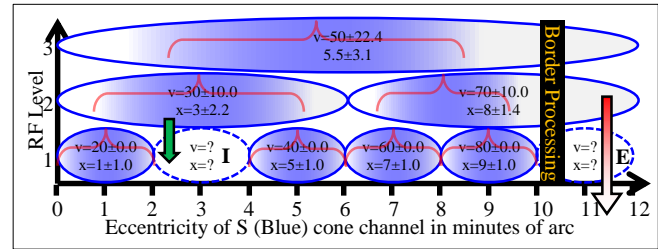


Figure 9: Interpolation vs. (no) Extrapolation. Showing the mean of each RF value  $\pm 1$  standard deviation.

simplified. ECM demonstrates that network circuitry can be traded against representational circuitry.

## Summary

Pyramidal cells can have independent spiking dendritic sub-units. But even with passive dendrites, a single neuron is effectively a two layer network that can compute linearly non-separable functions (Cazé et al., 2013). For, example, they can perform convolutions (Cuntz, Haag, & Borst, 2003). Therefore, we should consider the functionality that dendritic processing offers before constructing connectionist networks to perform the same functions.

The ECM model presented in this paper takes advantage of the extra computing power afforded by dendrites to support the *maintaining information coherence* function. The model is based on the idea that it is better to complexify locally, so as to simplify globally. In this case, it offers up a neurobiological mechanism to explain the phenomenon of receptive field remapping.

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