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Shifting attention to dynamics: Self-reconfiguration of neural networks

Christoph Kirst[1], Carl D. Modes[2,3] and Marcelo O. Magnasco[2]

Abstract
In recent years, considerable evidence has accrued indicating that brain function can be flexibly reconfigured on the fly: many brain areas are capable of carrying out a variety of distinct functions and are able to switch between those functions in a context-sensitive, dynamic fashion. Some evidence has also emerged that ongoing brain activity, the ceaseless background brain dynamics, may be implicated in setting and controlling these flexible functions as well as attentional gain. A crucial link between them is dynamics. Here we review both the accumulating evidence as well as propose a theoretical outline of dynamical mechanisms for functional self-reconfiguration of neural networks, including reconfiguration of logic function, reconfiguration of information routing, and poising at critical points to switch dynamics.

Addresses
[1] Kavli Neural Systems Center, Rockefeller University, New York NY, USA
[2] Laboratory of Integrative Neuroscience, Rockefeller University, New York NY, USA

Corresponding authors: Modes, Carl D; Kirst, Christoph
[3] Current Address: Max Planck Institute for Molecular Cell Biology and Genetics and Center for Systems Biology Dresden, Dresden, Germany.

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Introduction

Considerable mounting evidence has shown that the brain, in addition to retaining incredible amounts of long-term plasticity, can reconfigure certain operations “on the fly”, at speeds seemingly incompatible with lasting plastic changes in the underlying neuroanatomy. For example, intracortical interactions in primary visual cortex (V1) change dynamically during performance of specific acuity tasks [1]. In parallel, the rise of high-throughput technology to study global brain activity (hdEEG, MEG, ECoG) has uncovered information being exchanged between brain areas on an “as needed” basis during tasks and resting states [2–6]. From such observations, the notions of functional and effective connectivity emerged to describe situations where individual functional units can exchange information through dynamically-changing channels [7–10]. Even the functional identity of areas changes dynamically; for example V1 displays a large variety of cross-modal responses [11,12]. This suggests information moves within the brain in much the same way a telephone conversation can occur between any two telephones (functional connectivity), through a network of dedicated lines and routing switches (neuroanatomical substrate). **The aim of this paper is to review some of the evidence, and explore the theoretical implications that ongoing brain activity is implicated in the dynamic reconfiguring of neural function.** We posit that a central link between ongoing activity and functional connectivity is given by the dynamical systems nature of the neural circuitry.

The idea that the static structure of an information processing circuit might be dynamically affected by its own operation is not new [13,14]. An important technology in the world of silicon is the *field-programmable gate array* (FPGA), which had its genesis in the mid 80s [15]. An FPGA has two layers; the *circuit layer* contains an array of logic blocks and a massive set of wires (interconnect). The *control layer* has memory bits whose logic state controls the connections on the circuit layer: a given bit may control whether a specific wire in the interconnect is connected to the input of a certain gate. Therefore, writing to the memory of the control layer effectively creates (*instantiates*) hardware circuits in the circuit layer: “software” becomes hardware, the circuit operates at hardware speeds.

A“brain as FPGA” analogy may hold some usefulness for understanding flexible function and context-dependent processing in biological circuits, just like the “brain as computer” paradigm has had its usefulness. Nevertheless some distinctions must be made quite clear. First, there is no evidence whatsoever that the brain is reprogrammable into *arbitrary* circuitry, like an FPGA. Second, as FPGAs are used for reprogramming only rarely, the control layer is essentially quasistatic, and does not leverage any inherently dynamical properties. If the control layer needed to be dynamical, then each wiring configuration would have to be implemented via a fixed- or meta-stable point in a multi-stable dynamics. For example, imagine we want to switch between two distinct computational dynamics $\dot{x} = g(x)$ and $\dot{x} = h(x)$. A function $f(x, y)$ interpolating between g and h can be constructed so that $f(x, 1) = g(x)$ and $f(x, -1) = h(x)$, and then controlled with a variable y having ± 1 as its fixed points:

$$\begin{aligned} \dot{x} &= f(x, y) \\ \dot{y} &= y - y^3 \end{aligned}$$

Hence, the pattern of activity in the control layer y would dictate the effective dynamics of the circuit layer x. Appropriate feedback from that layer back into the control layer would turn this system into a self-modifying network. We here propose that such self-modifying systems, or "dynamically reconfigurable neuronal networks" (DRNNs) provide a powerful approach for the design of artificial networks and for understanding complex neuronal circuits in the brain.

In 'classical' approaches to neuronal computation the connectivity of a network is learned or modeled in order to perform a specific function and the network dynamics simply follow. This paradigm underlies many successful approaches in early sensory processing (e.g. Ref. [16]). In the last few years, this same approach has been deepened, and has met with spectacular success in the form of deep networks that in specialized tasks already exceed human performance [17–19]. Deep networks have even been proposed to underpin the inner workings of the brain [20–22]; however, though they are dynamical systems, they are often feed-forward dominated and make little use of the potential for computation that lurks in the rich dynamics recurrent networks are capable of producing [23–29]. These self-organizing collective dynamics – in contrast to simply reflecting the networks computation – have recently come under consideration as facilitating coordination and organization of flexible function [2,3,9,10,30,31]. Biology, propelled ever forwards in an endless evolutionary arms race, is loathe to leave such potential untapped [32,33]. General intelligence, solving generic tasks or being able to bootstrap function from a small set of samples, likely requires the interaction of a large number of subnetworks [22,34,35] which must coordinate communication and computation [9,36,37]. How can self- organizing dynamical processes be leveraged to improve such technology? And could our understanding of brain function be further bolstered by emphasizing these dynamical properties, both conceptually and in data analysis?

In biological information-processing networks, self-modifications of circuits operate on a broad range of time scales ranging from milliseconds to years and are mediated by a breadth of mechanisms [38]. Prominent and widely studied among these include synaptic and neuronal plasticity [39], other transcription-based modifications [40], adaptation [38], and homeostatic phenomena [41], often caused by a wide range of neuromodulators [42,43]. Plasticity as a dynamical process can be modulated itself via meta-plasticity [44]. On faster time scales, however, switching between different computations, context dependent processing, or rapid shifts of attention have all been shown to modulate local neural responses, but cannot be fully explained by these mechanisms alone. In this review we focus on how intrinsically-generated collective dynamics can establish DRNNs.

State dependent processing in neuronal circuits

Neuronal circuits compute information in a largely distributed fashion, displaying a variety of collective dynamics [23–29,45–48] ranging from highly synchronous states associated with pathological symptoms [49] to highly irregular asynchronous dynamics [50], e.g. due to balanced excitation and inhibition [51]. Besides widely observed oscillatory activity [52–57], other phenomena include wave-like dynamics [58], switching between up and down states [59] and other forms of multi- and meta-stability [2,3,5,60], inherent random dynamics [61], latching and sequence generation [62], self-organized criticality or avalanche-like dynamics [63], and chaos [64]. Given this range of collective dynamics, the question arises whether they emerge as a by-product of the network computing or whether they have deeper functional significance?

Huge experimental progress in recording activity from large populations of neurons [65,66] and even whole brains [67,68], has provided a wealth of new evidence for network-state-dependent processing [27,69,70]. In the worm *Caenorhabditis elegans*, the variability of the response of a sensory neuron to odors is modulated by the state of small subsets of neurons [71]. Distinct brain-wide activation states (akin to pre-defined execution protocols) have been identified in lower dimensional embeddings and linked to specific behavioral patterns [72,73]; in this representation a resting-like brain state shows increased fluctuations that could mediate flexible behavioral sequence generation. In whole brain recordings of zebrafish larvae [67] transitions between different neuronal activity patterns are observed in response to different stimuli or contexts [74]. In fly brains, motor feedback can affect the gain of visual processing [75]. In mammals, selective attention, task-specific information, and motor feedback can affect sensory processing in visual cortex [76–78]. Signatures of state- and context-specific computations have been observed in monkey motor cortex [79], resembling the