How Should Intelligence Be Abstracted in AI Research ...
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Models of Brains: What Should We Borrow From Biology?

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Abstract

Traditional models of neural networks used in computer science and much artificial intelligence research are typically based on an understanding of the brain from many decades ago. In this paper we present an overview of the major known functional properties of natural neural networks and present the evidence for how these properties have been implicated in learning processes as well as their interesting computational properties. Introducing some of these functional properties into neural networks evolved to perform learning or adaptation tasks has resulted in better solutions and improved evolvability, and a common theme emerging across computational studies of these properties is self-organisation. It is thought that self-organizing principles play a critical role in the development and functioning of natural neural networks, and thus an interesting direction for future research is explicitly exploring the use of self-organizing systems, via the functional properties reviewed here, in the development of neural networks for AI systems.

1 Introduction

There is a chasm between two established fields which commonly create artificial neural network models. Computational neuroscientists are, by definition, interested in creating models that are functionally realistic, with respect to natural neural networks, with a focus on the elucidation of the computational and information processing properties and functions of the neural network structures being modelled. On the other hand, most machine learning and artificial intelligence researchers are generally not concerned about such realism, opting for neural network models that, while biologically inspired, are typically based on an older, more simplified model of the brain – for example using a rate-based encoding scheme for neuron action potentials rather than a spiking model.

Recent decades have seen a great advancement in our understanding of the brain, including low-level and high-level computational and information processing phenomena. This, together with increased computational power, provide the opportunity to explore a range of more sophisticated neural network models than were feasible in the past. To what extent are the mechanisms underlying these newly observed phenomena beneficial, and what can these more sophisticated models offer in terms of the creation of artificially intelligent systems? This question drives to the heart of the overarching question: *"How Should Intelligence be Abstracted in AI Research?"*

This paper provides a brief review of the major known functional properties of natural neural networks. Where available, evidence of how these properties have been implicated in learning processes are presented, as well as related computational properties. It is hoped that this review can provide a useful launching point for artificial intelligence researchers interested in experimenting with more sophisticated neural network models.

2 Functional Properties of Natural Neural Networks

The exact functional properties of natural neural networks are complex and vary across brains from different species, brain regions and between different neuron and synapse types. The significance of various properties in learning processes, and why they are important, is not always clear. Some properties seem obviously significant, for example synaptic plasticity, while others could just be the result of evolutionary happenstance.

2.1 Neuromodulation

Neurons influence other neurons in two main ways: by sending electrical signals via synapses to other neurons, and by releasing neurotransmitters that diffuse into regions of the brain that affect, or modulate, the operation of many neurons and/or synapses.

There is evidence that some neuromodulators – affecting synaptic plasticity, neuronal spiking and synaptic transmission reliability – represent the learning parameters of learning systems in the brain, including reward prediction error, reward prediction time-frame, randomness of action selection, and learning rate (synaptic strength change rate) (Doya 2002; Seung 2003). This result and the numerous functional ramifications listed under specific properties below indicate that neuromodulation is strongly implicated in learning processes in natural neural networks.

2.2 Neuronal Action Potentials (Spiking)

Neurons receive input from other neurons, thereby changing the polarisation level of the neuron. If a neuron becomes sufficiently depolarised, according to a threshold value, it gen-

erates an action potential. An action potential is a very brief and sharp rise (spike) in the electrical output of a neuron, which is transmitted to other neurons via synaptic connections. Excitatory inputs depolarise neurons and inhibitory inputs repolarise them. Typically a neuron will not be able to spike again for some period of time after spiking (thus setting an upper bound on spiking frequency), this is known as the refractory period. Different neuron types have different refractory periods, and the refractory period may be influenced by the action of neuromodulators (Weinreich and Wonderlin 1987). An approximation of this spiking property that has traditionally been implemented in artificial neural networks is to generate an output on every discrete simulation time-step based on transforming the summation of the current input with a non-linear activation function (typically a Sigmoid function). Thus the output value can remain high, or be somewhere between high and low (depending on the activation function) for many consecutive time-steps. The underlying assumption of this approximation is that no information is encoded in the timing of spikes and instead that the overall frequency, or *rate*, of spikes is how information is encoded. These interpretations are known as timing- or spike-based and rate-based encoding (Kempter, Gerstner, and van Hemmen 1999).

The timing of spikes has many functional consequences and has been strongly implicated in various learning processes, see section 2.3. Mathematical analysis of typical Sigmoidal rate-based network models and integrate-and-fire spiking network models indicates that the latter have equal or greater computational power, depending on the function to be performed, compared to the former (Maass 1997). Finally, different neurons exhibit different types of spiking dynamics given the same input, many of which could perform computational functions (Izhikevich 2004).

Modulation of Neuronal Spiking Slow inactivation, also known as spike adaptation, of neurons occurs when a neuron has repeatedly spiked within a short time-frame, and effectively increases the spiking threshold (Cantrell and Catterall 2001). Neuromodulators can adjust the threshold at which a neuron will spike, making the neuron more or less likely to spike given the same amount of excitatory and inhibitory input in the same time frame, implementing a type of gating mechanism (Cantrell and Catterall 2001; Heckman et al. 2009). Neuromodulation can also influence spike adaptation, disabling or enabling it (Katz 1998). There is some evidence that modulation of neuronal excitability plays a role in learning processes (Daoudal and Debanne 2003; Saar, Grossman, and Barkai 2001).

2.3 Synaptic Plasticity

Synapse efficacy changes over time as a result of the activity of the pre- and post-synaptic neurons (Bliss and Lømo 1973). Traditionally, synaptic plasticity was studied under the assumption that the timing of spikes was not important, and instead only the rate of spikes was significant (Dan and Poo 2004; Roberts and Bell 2002). Later work found that synapse efficacy changes over time as a result of the relative timing of action potentials in the pre- and post-synaptic neurons (Bi and Poo 1998; Markram et al. 1997) (known as spike-timing-dependent plasticity, or STDP). For example, (Bi and Poo 1998) showed that, for some synapse types, a pre-synaptic spike followed closely by a post-synaptic spike – on the order of 5 to 40ms – increased synaptic efficacy.

Later studies have found that the relationship between spike-timing and synaptic plasticity varies greatly for different neuron and synapse types. For example, some relationships have longer or shorter time frames, some are the inverse of that described above, some are symmetrical (depending only on the absolute spike-time difference and not which neuron spiked first), some only induce synaptic depression, and some only depend on one neuron spiking (Roberts and Bell 2002). Additionally, for some synapse types, triplets or quadruplets of spikes do not integrate linearly in a simple summation of potentiation or depression effects (Froemke et al. 2006; Pfister and Gerstner 2006), but integrate non-linearly, for example the potentiation event may override the depression event in a post-pre-post spike sequence (Wang et al. 2005).

It is thought that synaptic plasticity is the primary mechanism for storing long-term memories (Cooke and Bliss 2006; McHugh et al. 1996). There is a wealth of evidence indicating that STDP plays a critical role in how neuronal circuits are formed and change over time (Dan and Poo 2004; Fiete et al. 2010; Kempter, Gerstner, and van Hemmen 1999; Izhikevich 2006). It has been shown that an STDP rule matching observed behaviour in natural neural networks not only reproduces the computational properties of the Bienenstock-Cooper-Munro (BCM) rule – which has been shown to maximize the selectivity of post-synaptic neurons – but is additionally sensitive to higher-order spatio-temporal input correlations (Gjorgjieva et al. 2011).

Plasticity of Synaptic Plasticity (Meta-Plasticity) The plasticity of synaptic plasticity can be modified in several different ways. Functionally, these differ in the time-scales in which they operate, which synapse types they affect, and how they modify the plasticity rules.

Plasticity can be influenced by the strength of a synapse, for example (Bi and Poo 1998) found that in some synapse types the amount of potentiation decreased as synaptic strength increased (while depression was unaffected by synaptic strength). Simulation experiments using models incorporating this potentiation damping mechanism were found to induce more stability in the system and result in synaptic strength distributions similar to those found in natural neural networks (van Rossum, Bi, and Turrigiano 2000). (van Rossum, Bi, and Turrigiano 2000) argues that weight-dependent potentiation creates a stabilising effect by directly counteracting the tendency of weights to saturate. Information theoretic analysis of soft-bound synaptic strength limits such as this have found that it increases information storage capacity using Hebbian plasticity rules for a set of synapses as compared to hard-bound limits (van Rossum, Shippi, and Barrett 2012).

Synaptic plasticity can be influenced via neurotransmitters, for example synaptic plasticity rules may only be enabled when a certain neuromodulator is present (Gaiarsa,

Caillard, and Ben-Ari 2002), or an asymmetrical STDP rule may be inverted in the presence of a neuromodulator (Huang et al. 2012; Seol et al. 2007). Potentiation can be enhanced by neuromodulators tens of seconds after the potentiation event (Otmakhova and Lisman 1996). Computational models have shown that such a mechanism can be used to solve the "distal reward problem" (Izhikevich 2007), where a reward signal can arrive several seconds after performing the action that led to it.

Plasticity can change as a result of pre and post-synaptic activity (Chen and Bear 2007) and as a function of the age of neurons (Zhao, Deng, and Gage 2008).

Since synaptic plasticity appears critical to various learning processes, as discussed above, then by extension systems that significantly affect the functioning of this property also seem likely to be utilised in learning processes. There is evidence that meta-plasticity mechanisms, including most of those listed above, are required for putting neural networks into learning states and stabilising learning and memory processes (Abraham 2008; Bailey et al. 2000), and various studies have found that incorporating simplified models of plasticity modulation have made it easier to evolve neural networks that perform online learning (Soltoggio et al. 2008; Silva, Urbano, and Christensen 2012).

Synaptic Scaling and Competition Mechanisms for inducing competition between synapses for efficacy have been observed in natural neural networks, such that the total synaptic efficacy among either incoming or outgoing connections is maintained at an equilibrium (Fonseca et al. 2004; Royer and Paré 2003). This has significant functional consequences. In (Abbott, Nelson, and others 2000) it is noted that proportional heterosynaptic scaling based on the post-synaptic spike rate seems to result in an optimal form of input selectivity related to the statistical method called principal component analysis. A similar mechanism is used to regulate neuronal action potentials such that they are maintained at an optimal level, for example for maximal memory capacity (Chechik, Meilijson, and Ruppin 1999).

STDP alone tends to result in tight, bunched synchronisation in initially random neuron populations, both spatially and temporally, with a few a winning "hub" neurons becoming drivers for the rest of the network (Fiete et al. 2010), resulting in networks with very short synaptic chains and activation sequences. However, models that also incorporate heterosynaptic competition result in networks forming multiple, scale-free synaptic chains with a distribution of lengths that match those found in some parts of natural neural networks (Fiete et al. 2010).

2.4 Stochastic Synaptic Transmission

Synaptic transmission is not always reliable, with some synapse types failing to transmit up to over half of presynaptic spikes (Allen and Stevens 1994). It has been proposed that synaptic unreliability allows for a kind of probabilistic reinforcement learning mechanism (Seung 2003). Neuromodulators may affect the reliability of synaptic transmission, however it not yet clear what functional significance this has (Bucher and Goaillard 2011).

2.5 Synaptic Transmission Delays

The time taken for an action potential to propagate from one neuron to another along an axon can vary considerably. Notably, the length of the synapse is not the only factor: the transmission speed can vary from 0.3m/s (Evarts 1965) to 120m/s (Telfeian and Connors 2003). At least some of this variation of conduction speed can be accounted for by metabolic and space constraints (Wang et al. 2008). However, there is empirical evidence that conduction delays are utilised for synchronising spiking between proximal and remote regions of the brain (Chomiak, Peters, and Hu 2008; Sugihara, Lang, and Llinas 1993). Theoretical studies have found evidence that synaptic transmission delays enable some useful computational properties, for example a model incorporating synaptic transmission delays and STDP exhibited a memory capacity greater than the number of neurons in the network (Izhikevich 2006) by self-organizing into polychronous groups.

Neuromodulators may affect transmission speed, however it is not clear what functional significance this has (Bucher and Goaillard 2011).

2.6 Synaptogenesis and Pruning

Synaptogenesis in natural neural networks is contingent on several factors. A dendrite must form "spines" to allow a synapse to form, at the site of a spine, between the dendrite and an axon from another neuron. Generation of spines is regulated by neuronal activity and the presence of various neurotransmitters, for example by controlling whether spines are created and the rate at which they grow and retract over different time scales (Akaneya et al. 2010; Saneyoshi et al. 2008). For at least some neuron types, dendritic spines of new neurons preferentially connect with axons which already have many connections, whereas spines of mature neurons preferentially connect with axons which do not have many connections (Toni et al. 2007). Synaptogenesis has been strongly implicated in learning processes in the brain (Black et al. 1990; Kelsch, Sim, and Lois 2010).

Synaptic pruning – the removal of synapses – occurs primarily via axon retraction (Luo and O'Leary 2005) and neuronal apoptosis, where synapses associated with the dead neuron are necessarily removed. Synaptic pruning may be used to remove synapses that are not functionally useful or appropriate (Vanderhaeghen and Cheng 2010).

Neurons and their axons and dendrites are situated in a three dimensional Cartesian space. Axon and dendrite growth and retraction, direction and branching within this space has been found to be influenced or directed by the presence of various neurotransmitters (Myers and Gomez 2011; Petros, Bryson, and Mason 2010). Additionally, axons and dendrites will only synapse with those from specific neuron types, as implemented by "adhesion molecules". These mechanisms have been found to implement functions such as self-avoidance and neuron identification, that is, the ability to connect to the "right" neuron or neuron type (Fuerst and Burgess 2009).

2.7 Neurogenesis and Apoptosis

In some regions of adult mammalian brains new neurons are created and are integrated functionally into the existing network throughout an individual's life (Zhao, Deng, and Gage 2008). Several regions in natural neural networks containing progenitor cells produce various types of neurons. After genesis neurons migrate to other areas in the brain (Zhao, Deng, and Gage 2008) and spatially distribute themselves with respect to the same and other cell types using molecular mechanisms for neuron type identification, adhesion and repulsion (Cantrup et al. 2012; Fuerst and Burgess 2009) similar to those used in synaptogenesis.

Neurogenesis is activity-dependent (Deng, Aimone, and Gage 2010), specifically, it is regulated by the presence of neurotransmitters and has been observed to increase when neuronal firing rates increase (Li and Pleasure 2010; Zhao, Deng, and Gage 2008). Apoptosis can occur if a new neuron is not sufficiently integrated into the network within some time window (Kitamura et al. 2010).

Neurogenesis has been implicated in learning and memory (Deng, Aimone, and Gage 2010; Zhao, Deng, and Gage 2008). For example, the number of neurons in a brain area associated with a particular task increases with increased practice or proficiency in the task (Black et al. 1990). Other experiments have found that performance in a difficult discrimination task improves when neurogenesis is boosted (Alonso et al. 2012), and becomes impaired when neurogenesis is ablated (Clelland et al. 2009; Goodman et al. 2010). The latter result is possibly due to a reduction in the amount of detail stored in new memories as no new neurons are available to become specialised to recognise unfamiliar input patterns (Aimone, Deng, and Gage 2011). While it should be noted that the exact role of neurogenesis in learning and memory is far from clear (Deng, Aimone, and Gage 2010; Li and Pleasure 2010), it appears that its role is nevertheless significant.

3 Discussion

Many functional properties in natural neural networks are implicated in learning processes or have other useful computational properties. Natural neural networks are extremely complex dynamical systems with myriad functional properties that directly or indirectly influence each other. Question that arise from this are whether these properties can be usefully incorporated piecemeal into artificial neural networks, and at what level of abstraction. These are largely open questions, however many of the theoretical and computational experiments referenced in this review incorporate only one or two properties at an abstract level and clearly demonstrate the utility of these properties in the form of useful computational or structural results. Additionally, several studies have found that introducing functional properties observed in natural neural networks, such as STDP and heterosynaptic competition, into neural networks evolved to perform learning or adaptation tasks can produce higher quality solutions, enable new capabilities, and improve evolvability (Hoinville, Tapia Siles, and Hénaff 2011; Di Paolo 2002; Soltoggio et al. 2008).

A common theme emerging across the computational studies is self-organisation. Many of the functional properties reviewed here, when incorporated into artificial neural network models, result in networks that self-organise in interesting ways. For example, heterosynaptic competition results in networks forming multiple, scale-free synaptic chains (Fiete et al. 2010), and a model incorporating synaptic transmission delays and STDP self-organises into polychronous groups, or "synfire" braids (Izhikevich 2006). It is thought that self-organizing principles play a critical role in the development and functioning of natural neural networks (Kaschube et al. 2010; Zheng, Dimitrakakis, and Triesch 2013). An interesting direction for future research could be explicitly exploring the use of self-organizing systems, via the functional properties reviewed here, in the development of neural networks for AI systems.

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