Spatiotemporal Coding in Cognition: an adaptive approach

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Introduction

The quest for developing a proper and complete account of intelligence is riddled with numerous conceptual hurdles and methodological difficulties. Although traditionally preoccupied with finding solutions to these insofar as they are pertinent to human ability, cognitive science can, under certain criteria, be seen as the research project which more generally attempts to provide an explanation to those phenomena that enable a single agent to *adapt* to environmental constraints via *systemic processes*. Three important hallmarks of scientific investigation make this interpretation sensible: evolution, development, and systems theory. Together, these can be used to establish research criteria that can lead to tremendous insight into the nature and functioning of cognizing agents. Interestingly, their common thread, as I will argue, lies in the notion of adaptation. What I aim to motivate in the following is that by framing investigations from an adaptive perspective a number of conceptual and methodological difficulties become more accessible. In particular, after developing the notions behind the adaptive criteria of interest, I will show how they can conveniently lead to the discovery of mechanisms which provide solutions to intelligent tasks under realistic biological constraints. Especially relevant to my present research, by setting biological constraints of the right kind at the right level, I aim to show how the discovery of neural spatiotemporal coding schemes as candidates for solving a broad range of behavioural and cognitive problems becomes feasible while utilizing little a priori knowledge and making few assumptions. Importantly, by investigating fundamental causal mechanisms from an adaptive standpoint I hope to make it apparent how setting our research this way can offer considerably fruitful grounding for modern cognitive science research. In conclusion, I will investigate the limitations to the approach proposed herein and offer possible solutions with direct implication for research in neural information coding.

Evolutionary Adaptation

Because cognitive science is about understanding the real time processes involved in intelligent action, research has mostly been preoccupied with those mechanisms and principles responsible for these processes. Take for instance, memory storage and retrieval, problem solving, language processing, etc. But by restricting our understanding of the mechanisms of intelligence at this time scale we impede our ability to understand the structural and functional origin of these abilities and we exclude the possibility of discovering perhaps more efficient methods for the modeling of intelligent agency.

One of the most touted insights to have ever bestowed science is Darwin's theory of natural selection. Central to this controversial idea is the principle by which all living forms interact with their environment via a complex network of competition and cooperation (Darwin 1859). These dynamics along with the generation of new offsprings results in the variation and fine tuning of phenotypic traits among species. This fine tuning process is tantamount to the notion of *evolutionary adaptation.* Here adaptation takes place in the form of phenotypic transformation of a species over generations and the elimination of individuals which carry traits that are either unable or less efficient at coping with variations in their environment.

Today, a complete understanding of the complex interactions and conditions underlying evolution as it occurs in nature still hasn't been attained. The impact of genetic drift, problems of open ended evolution, and conditions giving rise to evolutionary network neutrality are amongst a number of challenging and intriguing contemporary topics in evolutionary theory (Barnett 1998, Cariani 2008). However, the basic mechanisms of evolution are today not only well understood but have also proven to be highly effective as a means to discover better system configurations, that is, to find increasingly better parameters for an expected operation (Holland 1975). Under this interpretation, evolutionary algorithms can effectively search through a parametric space in pursuit of global maxima [1] and successfully escape local maxima. This guaranteed convergence to better solutions under appropri-

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[1] The best parametric configuration available within the operational context of the system.

ate conditions has attracted many modellers. In particular, in virtue of the ubiquitous availability of computing, the implementation of evolutionary algorithms for finding better parametric solutions in this way is extremely facilitated.

Beyond the advantage of converging towards better solutions, evolutionary algorithms exhibit another outstanding feature that takes center stage in Darwin's theory of natural selection: new and improved system designs appear without the imposition of normative criteria. At most, the fitness criteria (or function), which defines a measure of success for the evolved species, sets *indirect* task conditions for which an individual should be preserved or discarded from the population. Fitness functions are indirect in two senses. In the first sense, they only measure success of individuals in comparison to other individuals of the same generation. This means that the algorithm is not constrained to follow any predetermined search direction. Second, because a system task is specified, any system configuration that can better approximate to that task has the potential of carrying valuable phenotypic traits. Importantly, indirect task conditions avoid two significant problems: first, if evolutionary algorithms imposed a measure of success based on some direct phenotypic criteria, the algorithm would cease to discover alternate and improved individuals as soon as an individual met those criteria. Second, given the complexity of the network of interaction between individuals and their environment, it is extremely difficult for a researcher to state a priori phenotypic traits that are being looked for. In fact, those traits are precisely what the researcher wants to determine in the first place. Fortunately, evolutionary algorithms can do so autonomously without direct supervision nor the use of a training set.

Modelling approaches that draw upon evolutionary techniques are thus more likely to find phenotypic solutions to a broad class of problems without having any prior knowledge of the kinds of parameters necessary to do so. In realistic experimental conditions, however, some inherent constraints due to the modelling techniques, theoretical frameworks, or system characteristics will inevitably have an effect on the obtainable results. In time dependent simulations, for instance, the experimenter will have to decide whether variable state changes are to be integrated at every time step or should instead be event driven. As another example, in neural modelling, it is often convenient to fix a certain number of parameters such as the number of neurones, or the activation function etc. so to limit the search space of the evolutionary algorithm. This allows for a quicker convergence towards the parametric space of value. Fortunately, these a priori conditions can usually be safely determined from empirical evidence or shown to be sufficiently sound to demonstrate the phenomenon of interest.

At the heart of evolutionary design lies a perhaps obvious but fundamental principle that deserves better appreciation: this principle is *phylogeny*. The inheritance of traits from previous generations suggests that some continuity in the genotype (and presumably phenotype) offers a mechanism for functional scaffolding. The evolutionary system doesn't need to 'reinvent the wheel' at each new generation so to improve its adaptive performance. What this means is that increased behavioural complexity exhibited by an individual during its lifetime is likely based on simpler structural qualities inherited from its ancestors. This inherent feature of evolutionary design constitutes not only a terrific asset from a design perspective but is also an invaluable conceptual tool. From a design perspective, this means that structures initially evolved to accomplish a certain task, can be used as the base population to be evolved for a new task. Dario Floreano, for instance, has shown how an initial generation of robots evolved to perform obstacle avoidance could subsequently be used to evolve a population that would not only preserve the ability of avoiding obstacles but also manipulate objects in the environment (Floreano 1998). Conceptually, what this tells us is that by employing an evolutionary approach, complex phenotypic traits can often be broken down into a discreet[2] sequence of increasingly complex structures with their corresponding functions[3].

An evolutionary approach can thus be extremely helpful in the investigation of 'possible-world' systems that are effective in accomplishing the task for which they are selected. If Darwin is correct, cognizing agents have also achieved their contemporary abilities via similar evolutionary processes: their phenotypic traits have been selected for in virtue of their adaptation to their environmental conditions. But as I've attempted to portray, any system that undergoes evolutionary change (e.g. a population of agents) in fact exhibits a form of learning whereby changes in the environment are accompanied by adaptation of the system to those changes. This mechanism actually reveals how structures, despite being fixed during the lifetime of each individual of the system, can undergo change at the timescale of generations. Because, spatiotemporal phenomenon in the nervous system of animals (including humans) have functional significance that is still poorly understood, it is equally difficult to determine the structural conditions under which they may arise with respect to their functional role. Yet, by

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[2] At least epistemically discreet and perhaps not ontologically.

[3] Note, however, that it doesn't necessarily follow that a degree of structural complexity corresponds to a proportional degree of functional complexity.

employing the principle of phylogeny offered by and evolutionary approach along with its minimal requirement for design assumptions, it should become increasingly clear how an elaborate yet rigorous account of the functional role of spatiotemporal neural processes can be achieved. Before establishing in greater detail the criteria that must be met for success, it is important to first develop a better understanding of another fundamental mechanisms that tie intimately with this phylogenetic principle yet lie at an entirely different timescale; these are mechanisms that occur during development.

Developmental Adaptation

Despite more than 200 years of biological investigation into the mechanisms involved in the growth of living organisms, cognitive science has payed virtually no attention to the insights this work offers with respect to our understanding of the structural and functional origin of the processes involved in cognition. Although significant records have been made regarding the developmental stages of numerous species, one of the most insightful works attempting to reconcile these findings into a structural and mechanistic theory of development is that of Sir D'Arcy Thompson. In his work 'On Growth and Form', Thompson aims to motivate the importance of development in determining the ultimate form of a mature organism (Thompson 1917). According to him, the amazing complexity involved during growth implies that a set of fine tuned mechanistic processes must play a role nearly as important as evolution in determining the final structure which leads to complete function. Although Thompson's work lacked any causal account of the principles of growth, his work inspired many. Interestingly, in the 50's, the often considered grandfather of artificial intelligence, Allan Turing made a significant contribution to the field of development with a formalism on the theoretical mechanisms of cellular morphogenesis (Turing 1952). In this work, Turing established the preliminary equations describing possible scenarios involved in cellular communication via chemical reactions and diffusions. In virtue of his insights, a large number of developmental phenomena could begin to be explained. For instance, pigment patterns on the coat of animals or on butterfly wings; the differentiation of cells with respect to their neighbours, etc. (Spemann 1938, Wolpert 1969). Ultimately, what this work illustrates is that not unlike evolution, the developing system is also determined by a complex network of localized interactions.

Development becomes especially interesting once we begin to understand the benefit that is may represent for the formation of the body and nervous system in animals. For instance, by respecting developmental timelines the growing brain is first determined at the level of its primitive functions; i.e. the brain stem for the regulation of vital functions, and is progressively complemented with parts decreasingly important for survival, such as the cerebellum for motion, the limbic system for arousal, and finally the neocortices for higher cognitive function (Kandel et al. 2000). Furthermore, histologic studies have shown how new cortical neural cells migrate from deeper tissue layers outwards to the surface of the growing brain (Purves and Lichtman 1985). Unfortunately, today, the functional roles of these layers in cognition are still not well understood. It is therefore difficult to assess the organizational importance of these kinds of structures and infer any kind of hierarchical role that they may play. Indeed, correlating structural hierarchies with functional hierarchies could lead to a much better understanding of the overall complexity of the mind. An important functional phenomenon that has been observed, however, is that of a neural 'winner take all' strategy during neurogenesis (Grossberg 1973). During neurogenesis numerous afferent connections enervate a target cell or receptive field, however, those connections that fire more frequently will be reinforced and preserved, whereas those signalling less will tend to wither and disappear. This positive reinforcement of active neurones is reminiscent of the well known Hebbian learning principle (Hebb 1949). The implication of this is that within a large population of neurones competition takes place between cells that connect to the same regions during development. Thus, similarly to the evolutionary principle mentioned above, this mechanism suggests that a high degree of local adaptation in brains takes place during growth.

In addition to this adaptive characteristic of development, another computational or generative advantage arises from these processes. Combined with evolution, development allows for a much greater degree of complexity to be encoded in the genotype. Indeed, by merely encoding the initial parameters of a single cell, the epigenetic processes involved in gene regulation and chemical reaction-diffusion allows a multi-billion cellular organism with massive cell specialization and complex structure to emerge after only a few months of growth (Wolpert et al. 2002). By taking advantage of this indirect encoding method, evolutionary algorithms combined with developmental processes could lead to a more comprehensible breakdown of the processes involved in modelling cognitive models. In particular, I will show in the next sections how the inherently spatial nature of structural development fits especially well with the prospect of investigating spatiotemporal properties of neural information coding.

Cognition as Adaptation

With the conceptual and methodological appeal of evolutionary and developmental approaches exposed, one can begin to see how their underlying systemic timescales occupy different regions of adaptation. While evolution occurs over the course of generations, development occurs over the course of months and years. What is of most common concern for cognitive science, however, is the understanding of those processes which take place over the course of seconds, minutes and perhaps hours; I call this the *topical* timescale. That is, the time scale at which perception, reasoning, and action take place. To better grasp the essential characteristics of the processes taking place at this timescale, it is useful to return to the origins of the systems view of cognition.

Upon the emergence of new technological tools and mathematical insights in the early 1900's the cybernetics movement drew inspiration from the challenges set forth by the prospect of understanding general system mechanisms and forms of control. With more emphasis on agency, Norbert Wiener, a pioneer in cybernetics, saw it as the the science of control and communication in animals and machines (Wiener 1948). Amongst one of its most prolific adepts, the psychiatrist Ross Ashby, contributed significant insights that resonate still today in the field of artificial intelligence, psychology and theory of mind (Ashby 1956). For instance, he articulated how the science of control and communication is based on fundamentally simple principles accessible to all without advanced knowledge in mathematics, biology or physics. He also emphasized the conceptual importance of focussing our analysis not on the nature of the device, nor on what it is made of, but on what it does, or what its behaviour or function is. In particular, he was interested in functions in so far as they were reproducible, regular or determinate (Ashby 1956, p.1).

In his 'Introduction to Cybernetics', Ashby develops with great detail the formal definition of a system applicable to artificial machines, biological organisms, or any other self-organized system (Ashby 1956). Broadly, his characterization encompasses the core notions behind linear and non-linear system characteristics and dynamics, such as, state transformations, feedback, stability and equilibrium, variety and transmission, and regulation. Amongst these, Ashby's sophisticated development of the notion and implications behind variability is perhaps the most influential in today's work on adaptive systems modelling. In particular, the principle of *Requisite Variety* exemplifies with elegance the fundamental difference between simple reactive agency, and complex behavioural regulation. Said simply, this principle states that in order for an agent to adapt to changes in its environment it must produce change in itself so to compensate with external variation. Thus variety is required to cope with variety. For instance, to compensate for the increase in external temperature, the mammal will generate sweat to cool its body; to avoid an incoming projectile an agent could move its limbs. Hence the agent disposes of parameters on which it can operate so to maintain a status quo between itself and the environment. Of course, many of these behaviours may count as simply reflexive, or simple regulations, with a fairly linear interaction between the point of sensation and that of action. But what Ashby noticed, is that complex behaviours occur because they must fulfill an ultimate task: survival. Hence, an agent cannot simply let constitutive parameters drift away indefinitely but must maintain those essential for survival within a stable tolerable range. From this notion he introduced the idea of a second degree regulation named *ultra stability*: behavioural or corporeal fluctuations constantly maintain critical parameters within viable limits (Ashby 1960 p.81). To do so this second degree system (system S) manipulates those mechanisms involved in basic first-degree interaction (system R) - see figure 1. The complex network of interaction between system S and R, and between R and the environment, as Ashby suggests, captures the essential characteristics that a system must meet for complex adaptive behaviour. Interestingly, with little more conceptual unpacking, it can be said those mechanisms typically interesting to cognitive science are those involved in system S; that is, those which enable an agent to develop complex 'scenarios' for the control of behaviour so to maintain critical bodily conditions within a stable viable range.

This simple yet powerful proposal by Ashby becomes especially relevant when we begin to understand the complexity of interaction occurring in the nervous system. These complexities offer the owner the ability to deliver countless number of varying solutions to a broad range of problems. By paying closer attention to the structural and functional principles of the nervous system it becomes increasingly clear how this can be mechanistically achieved.

The Physiological Roots of Neural Cognition

In his recent book 'Rhythms of the Brain', Buzsaki makes a particularly good case concerning the complexity of cognition from an anatomical and mechanistic viewpoint (Buzsaki 2006). With respect to structural complexity, Buzsaki elaborates a fruitful perspective regarding the connective

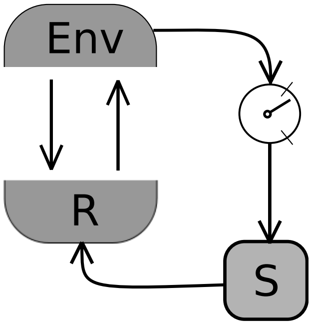

Figure 1: An ultrastable system with a first degree reactive system R, and second degree regulating system S. S manipulates R so to keep essential variables (represented by a dial) that are affected by the environment within viable range. Inspired from Ashby 1960.

topology of neurones and its functional significance. The estimated 10^{11} neurones in the human brain with their average 10^{3} afferent synaptic connections each, represents a priori and incommensurable network of firing activity. However, with the help of histological observations and mathematical abstraction, a more comprehensive account of the underlying functional significance of such an architecture can be made. Small localized networks of strong interaction are found as the predominant form of connectivity in the brain. Indeed, specialized brain regions and nuclei are characteristic of mammalian brains. However, strong interconnection between these regions is also necessary for useful coordination between regions to take place. According to Buzsaki, in order to exploit the benefit of having a small degree of separability between any two neurones in the brain while minimizing the spatial and anatomic cost of dense connectivity, evolution and development found a solution through what is known as 'small-world' connectivity (Watts & Strogatz 1998, Di Ferdinando et al. 2001, Buzsaki 2006 p.37). A small number of random connections can significantly reduce the degrees of separation between neurones, while dense local connections increase clustering and, by consequent, functional specialization - see figure 2. A high degree of connectivity is thus maintained at a relatively low cost.

In addition to advantageous structural conditions, the existence of diverse types of neurones, neurotransmitters and synaptic gates provides for a wide heterogeneity in localized function. Amongst the most important of these is the existence of two general types of synaptic modes: excitatory

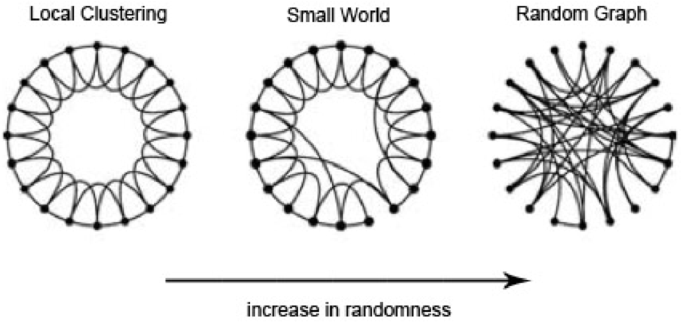

Figure 2: Small world topology in the centre in comparison to a local clustering graph where each nodes connect to their four neighbours, and a randomly connected graph. From Watts and Strogatz 1996.

and inhibitory. As Buzsaki argues, while excitatory connections coordinate and/or amplify propagated signals, they do so with ever-increasing activity and no possible stabilization on their own (Buzsaki 2006 p.62). However, inhibitory connections provide the interesting characteristic of 'disinhibition': if a first neurone A inhibits a second neurone B, and that second neurone B inhibits a third C, then inhibitory action of the first on the second promotes excitatory activity of the third. The third neurone C is thus disinhibited by the first A - see figure 3. Thus inhibitory connections can not only bring stability but also non-linearity to the population of nodes. Indeed, histological studies have measured an approximate 10-15% ratio of inhibitory connections in the mammalian neocortex (Abeles 1991, p.50-53).

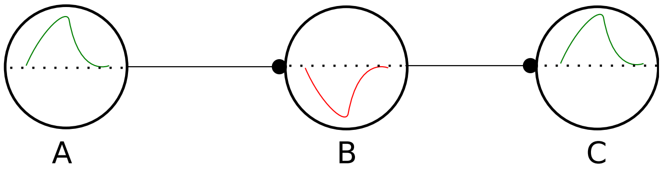

Figure 3: Two levels of inhibition where the first neurone A disinhibits the third neurone C.

This local stabilizing property within populations of excitatory and inhibitory neurones is an early reflection of the importance of Ashby's insight discussed in the previous section. In virtue of these local properties, the nervous system of an agent can regulate its activity by maintaining neural excitation within ranges of functional viability. For instance, the proper functioning of these mechanisms prevents the occurrence of dangerous high-activity neural states seen in epileptic seizures or in parkinson's disease. Of course, as mentioned earlier, cognitive scientists are interested in the more complex regulatory methods that endow an agent with the ability to perceive, think, and act. What the previous observations tell us, however, is that these complex cognitive aptitudes are inherently based on the fundamental capacity of neuronal structures that possess a set of simple local characteristics amenable to complex information processing.

Although the anatomical features just discussed hint to their functional role, neither topographical organization nor local activation properties elicit a strong enough intuition regarding the processes involved in perception, thinking, and action. Although animal cognition is fundamentally rooted in these features, it is important that we attempt to understand how the nervous system and body take advantage of these for intelligent action.

Neural Coding

In accordance with Ashby's view, the essence of the nervous system is to regulate environmental change through requisite variety and regulated stability. Underlying the mechanism of variety lies the fundamental role of systems: transformation. Generally speaking, this involves the change of the state of the system through some functional mechanism that belongs to the system itself.

In the most abstract approach to neural computation, the transformation of an input value to some output value in a single neurone is realized via an activation function (Rumelhart & McClelland 1986). If this activation method is non-linear the use of this method within a population of abstract neural cells can compute virtually any algebraic function. Various architectures based on this general method can perform important feats, such as associative memories, pattern completion, and discrimination. Although these features are arguably computationally complete with respect to any kind of functional description, it seems increasingly clear, that this level of characterization is not dynamically sufficient for an adequate account of second degree regulation as required by Ashby's system S. In particular it is unclear how internal network regulation can take place within these architectures such that state transience is maintained for the continued solving, prediction, and monitoring of physical or mental tasks. There are a number of dynamical features which standard connectionist models do not commonly exploit yet are present in their real biological counterparts. Two of these are significant and are becoming increasingly better understood. The first has to do with local self regulation, this is *recurrence*; and the second had to do with the timing of neurones within a group, this is *spatiotemporal coding*. As I will expose in the following, what both of these share is the ability to generate complex internal dynamics that may lead to the kind of processing necessary to account for complex second order regulation as in Ashby's system S.

The simplest form of abstract neural models are feedforward models where layers of neurones feed their connections to subsequent layers so to compute input-output functions. With a sufficient number of hidden layers and nodes these can solve any algebraic function. However, adjusting the weights between connected nodes requires that some external error be measured and applied to the individual weights. This is known as supervised learning (Churchland & Sejnowski 1992 p.115). Because information flows uni-directionally these are pure reactive systems. In recurrent networks, however, internal local feedback is provided from later layers to previous layers, from same layer cells, or even from a cell to itself. As Churchland and Sejnowski note, this endows a network with numerous capacities such as incorporating multiple time scales within the nodes, processing sequences of inputs that extend over long periods of time, generate rhythms at various frequencies, and resolve ambiguities. Because of these internal feedbacks, or re-entrant connections, and unlike simple feedforward networks, the processing in recurrent networks of subsequent external inputs is highly dependent on its previous internal state. Also, output in these networks can even change while the input remains unchanged. Hence recurrent networks are subject to significantly complex internal dynamics that not only transform input but can also independently generate output. Because these dynamics often exhibit a large number of non-linearities, it is common practice to employ a dynamical systems approach to analyze recurrent network behaviours and segregate them effectively. Unfortunately, as in their traditional feedforward counterparts, recurrent networks are typically agnostic to the temporal conditions found in the neurobiological substrate. More specifically, every cell in these networks integrate their input at the same time as every other cell. This leads to a total synchronous updating. Because the networks often employ real valued outputs, in correspondence to average firing rates, the amount of variability they can produce despite being fully synchronized is still significant (Churchland & Sejnowski 1992, p.164). However, there is a growing sense within the neuroscientific, dynamical systems, and artificial

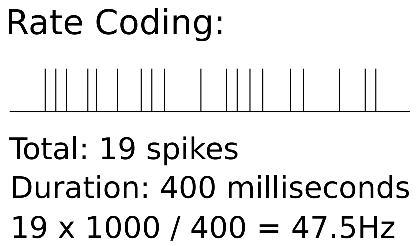

Figure 4: Rate coding is based on counting the number of spikes that occur during the psychological time of an experiment and deriving its frequency. Here, 19 spikes during 400ms leads to an averaged rate of 47.5Hz.

intelligence community that the temporal component of neural signalling may play a crucial role for the adequate capturing of higher order cognitive processes.

Due to sufficiency, simplicity, or plain ignorance the large majority of research in neuropsychology and in neural modelling for cognition has privileged rate coding as the fundamental mechanism of signal transformation - see figure 4. However, since von der Malsburg's suggestion in 1981 that neural populations can cooperate via synchronous firing, a growing interest in the potential of synchronous activity to solve various processing tasks has emerged - see figure 5 for a depiction of synchrony (von der Malsburg 1981). It is important, however, to note how from a neuroscientific perspective, neural activity is largely performed asynchronously. Thus according to this view, within a population of fixed interconnected cells, sub-populations can at times fire in unison within a larger population of asynchronously firing neurones. Although today, a number of experiments have shown that synchronous firing takes place during a number of cognitive tasks, such as visual processing, sensorimotor coordination, etc., none have shown why these spatiotemporal patterns present a processing advantage nor how they play a role in the larger cognitive picture (Fujii et al. 1996). The best hypothesis to date dates back since von der Malsburg who stated that synchrony may be the mechanism by which the brain solves the binding problem (von der Malsburg 1981). The binding problem addresses the condition in which a set of features available in the environment need to be spatially and temporally correlated within a population of cells. For instance, the simultaneous visual perception of a green square and a red circle will elicit the excitation of cells in the visual receptive fields for red, green, circle, and square at the same time; but how is the perception of green correlated with the perception of a

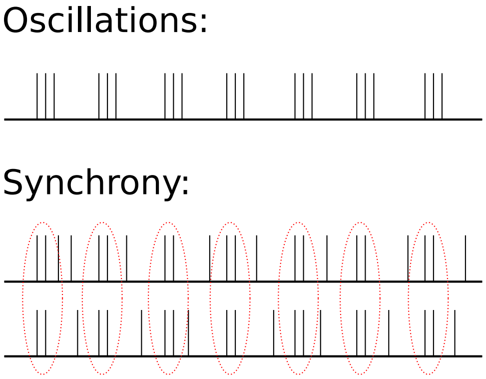

Figure 5: Oscillations occur when a neurone or a group of neurones fire between regular periods of time. Synchrony between two or more neurones occurs when they occasionally fire at the same time, as illustrated above, or sometimes even out of phase.

square, and the perception of red with the perception of a circle? To solve this, synchronous firing in a population could be used. By having green and square cells fire synchronously, and red and circle fire synchronously, target cells, perhaps responsible for conscious representation, could detect the correlation of the shapes with their respective colours - see figure 6.

Signal binding based on spatiotemporal mechanisms represent a form of transient coordination and association between cells. Functionally productive local soft assemblies can emerge on top of a large hardwired network of cells so to control the activation of role specific cells or recruit new cells via dynamical entrainment. Interestingly, given the amount of neurones in the brain the the possible combination of synchronized groups at various frequencies suggests that spatiotemporal coding could better account for the parallel processing of different events at different time scales at the same time. Mechanisms of divided attention such as driving a vehicle while speaking with a passenger may thus become increasingly better understood from a neuro-systemic viewpoint.

More recently, neuroscientific interest in spatiotemporal coding is leaning towards the notion that the brain's use of this type of coding isn't limited to synchronized rhythms but that it may perform more subtle computations based on a general ability to exploit the precise timing of spikes (Fujii et al. 1996; Izikevich 2006). In virtue of a neurone's sensitivity to the amount of incoming signals it receives, it can become an effective coincidence detector

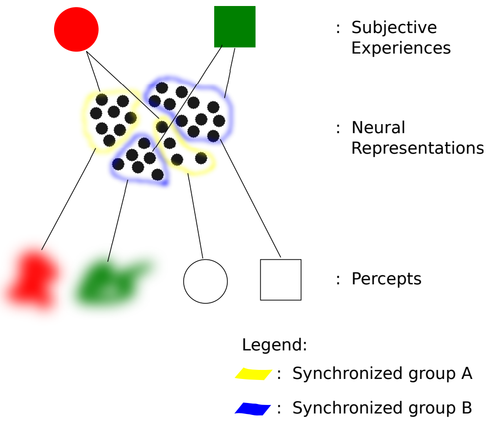

Figure 6: Feature Binding: the distinct colour and shape features are encoded by individual populations of neurones. When a colour population fires synchronously with a shape population then the coloured object is experienced. Here, group A fires synchronously (e.g. 45Hz) to subjectively represent a red circle, and group B fires synchronously (e.g. 62Hz) to represent a green square.

- see figure 7. Coincidence detection occurs when a neurone only fires when two or more incident signals trigger simultaneous post synaptic potentiation. Hence the time of firing of the source neurones is only relevant insofar as it affects the time of incidence of the incoming spikes on the target neurone. This timing is especially contingent on the firing time of the source neurones and the propagation delay of the signal to the target. Gross measures of synchrony at the somatic or axonal levels may then only expose a subset of interesting spatiotemporal coding phenomena. Instead, a measure of the synchronous activation of synapses should reveal the true presence of coincidence detection. This so called polychronous activity could thus form a supplementary form of coding to that of rate coding for perception, thinking, and action.

As discussed above, detecting the correlation of spatiotemporal activity with certain behaviours and perceptual stimuli can only give us a limited account of their causal role. In particular, it is especially difficult to understand their underlying function and make predictions of their effect from these observations alone. Logical hypotheses, such as feature binding, provide theoretical starting points for exploring their causal role. To complete our understanding of their role, however, it is necessary that we develop

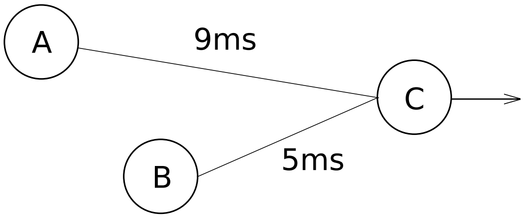

Figure 7: Coindcidence Detection: A source neurone A connects to a target neurone C with a 9ms delay, and a source neurone B connects to target C with a 5ms delay. If neurone C requires the combined signals from A and B to fire, then C will only fire if B fires 4 milliseconds after A. C thus 'detects' the coincidence of incoming signals.

an adequate experimental method which permits a careful assessment of the information transformational role that they play in realistic embodied cognitive tasks. I motivate this in the following section.

The Neural Adaptive Advantage

To gain a thorough understanding of cognition it is necessary that we address the complex processes taking place in at a neurobiological level. With the increase awareness of the complexity underlying natural biological processes, it is becoming more clear how there is a large class of problems for which there is no easy formal analysis or proof. If the degree in non-linearity of a dynamical system is too high, this system is indeed nearly intractable from a formal mathematical standpoint (Beer 1995). Given the already observed complexity of simple neurally inspired systems, it is clear that this doesn't get any simpler in larger neural systems such as the human brain. Fortunately, modern computational modelling permits a very new type of science to be exploited for this. Simulation is a method of investigation that permits the verification of formal models from a very useful behavioural standpoint. By computationally implementing those parameters and relations capturing the hypothetical functional criteria of a system it is possible to derive, given initial conditions, a complete portrait of the system's change over time. This can then be compared to its natural counterpart for validation.

With respect to neural coding, hypothetical parametric conditions can be designed and tested against realistic stimuli. If internal neural behaviour and external bodily actions match predictions then the model is supported.

Given the high order of complexity, however, determining a set of parameters which will give rise to expected behaviour can become an arduous task, and nearly impossible from a practical standpoint. Furthermore, attempting to address this directly in systems such as bodies and nervous systems where modularity and functional layering are cardinal to their correct operation, capturing the dynamical complexity of a part of a system for a specific task may in fact be counterproductive in that once integrated within a larger context, those previously valid parameteric conditions no longer apply. Fortunately, to address this, the adaptive approach has, as I have illustrated in the early sections, established a profound understanding of the three fundamental timescales on which adequate parameters and structural configuration are established in real neural agents: evolutionary, developmental and topical.

Structurally, evolution provides transient genetic fixation and regulation with respect to environmental variation. This amounts to a form of learning over generations. With respect to parameters, evolution can explore a broad landscape of configurations and is capable of discovering novel solutions to ill defined problems. Development provides a phenotypic layer of encoding which not only amplifies the expressibility of the genome, but provides stability through staged growth processes. In virtue of this, complex layering can be grounded on more simple layers, providing a progressive scaffolding for enhanced behaviour. Thus, appealing to an evolutionary and developmental approach to modelling can provide a significant advantage for the generation of structural and functional hypotheses. Interestingly, this approach is particularly appropriate for exploring spatiotemporal codes of cognition.

Because spatiotemporal codes of the coincidence detection type inherently depend on the asynchrony of network dynamics and delay of connections, structural conditions are fundamental to their proper functioning. Hence employing evolutionary methods for parameters exploration coupled with developmental processes for structural organization constitutes a highly effective methods for the iterative exploration of models with increasing spatiotemporal complexity and increasing behavioural complexity. Although complex behaviour may naturally follow from complex internal processes, it is useful to distinguish the class of dynamics to which either belong and examine how they compare. This can be accomplished by initiating research with simpler architectures, progressively explore more complex tasks, and more sophisticated architectures. For instance, oscillations are simple temporal neural dynamics which may occur independently of group dynamics - see figure 5. The alternating activation of a few nodes can directly affect the behavioural performance of the agent which results in an adaptive advantage over non oscillating dynamics. Heerebout and Phaf, for instance, have shown how simple recurrent connections within a traditional feedforward network can give rise to internal oscillations that provide an artificial agent with the capacity to 'scan' for predators, by looking left and right, while foraging for food (Heerebout &Phaf 2009). These agents could then escape predators more quickly than their non oscillating counterparts. Simple oscillations can thus be viewed as early adaptive advantages over non oscillating solutions. This is especially more salient given that Heerebout and Phaf evolved the neural network parameters for these agents based on their fitness to 'eat' food. Indeed, within the first few thousand generations, basic non-oscillating dynamics allowed the agents to develop simple escape behaviours from predators and attraction to food, but by allowing the generations to evolve further a sudden jump in fitness occurred after a few more thousand generations when oscillations appeared. Hence, by employing this iterative approach via evolutionary and developmental mechanisms, it should be possible to re-create spatiotemporal mechanisms responsible for increasingly complex cognitive tasks and the structural modularity on which they are based.

Conclusion

Despite the major domination of rationalism in the recent history of cognitive science, the field still bears its deepest roots in the science of the observable. Its aim is to explain is the astounding intellectual feats realized by humans and other living systems alike. Because of this empirical grounding, cognitive science should rightfully vindicate its kinship to the biological sciences. Rationalism, instead, can be seen as one of the many methodological approaches to its investigation. From a biological perspective, research in cognition can thus take advantage of the conceptual tools and methodologies generally applicable to biology and its diverse systems. An early application of this can be found in developmental psychology. By studying the variation in psychological and linguistic ability during early stages of an individual's life, developmental psychologist are capable of ganing a better understanding of the stages though which new competences are acquired, and even at times infer their relation or dissociation to other traits and help form a greater picture of the underlying causal story. However, developmental psychology is still immature regarding its ability to provide some neural processing explanation for those competences discovered. This is especially made obvious by its continued use of age (usually in months) as averaged index in characterizing psychological traits, rather then employing the developmental status of neural structures or their functional qualities. It is thus becoming increasingly clear that causal explanations based on systemic structures and operations is needed in the field. Furthermore, adaptation fits well within the positivist and empirical approaches introduced by Comte, Locke, Hume and others (Compte 1896, Locke 1690, Hume 1739). Yet, the idea that perception, thought, and action are the result of a postiori regulations which only take place in the event of change is a hurdle for traditional positivist views. Indeed, sophisticated cognition happens to be highly creative, pro-active, and insightful. However, what Kant's idealist philosophy and the psychophysics of Weber, Helmholtz, Fechner and others led to discover, is that a large amount of a priori aptitude is made available from biological and nervous structure (Weber 1846, Helmholtz 1859, Fechner 1860). Yet, this empirical/rational discrepancy can be reconciled once one seems how the longer timescale in systems such as evolution and development, provide the necessary a priori conditions for the cognitive system to be a physiologically successful machine which leeds to a functional capacity for second degree regulation, or in other words, generative adaptation. What I have shown here, is that by adopting a modelling approach based on simulation, those conditions leading to complex adaptive behaviour can be discovered. In particular, employing an evolutionary and developmental approach to systems design, biologically plausible candidates that can solve complex cognitive tasks can be discovered, analyzed and interpreted in a way which provides insights never before attainable. Most importantly, the exploration of spatiotemporal codes in this manner can lead to the fruitful discovery of those internal conditions and external tasks in which they provide a definite adaptive advantage.

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