Modelling collective phenomena in neuroscience

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This paper shows how concepts and tools borrowed from statistical physics might be useful for modelling biological systems. This is illustrated by specific examples taken from the study of neural dynamics. The relevance for neuroscience of the notion of 'collective phenomena', for which statistical physics gives appropriate modelling tools, is discussed.

MODELLING ASSOCIATIVE MEMORY

Short-term memory is probably the simplest form of human (and not only human) memory. It also shows remarkable features that demand explanation, among which are:

- associativity: what has been stored in memory is retrieved from partial or related information. Unlike standard computer memory, human memory is thus a content-addressable memory (CAM) – interestingly, since the early 1990s, CAM hardware has been under development for internet routers, allowing for very fast processing[1]
- learning: working memory is permanently storing new events/objects, and this without getting doomed by its (necessarily finite) maximal capacity. This implies the ability to forget
- persistent neural activity: as shown by electrophysiological recordings in monkeys during delayed response tasks,[2] on short timescales a neural activity can be maintained while keeping its specificity to a stimulus despite the noise in the network dynamics.

In the late 1940s, Donald Hebb gave general qualitative accounts of neural organisation, dynamics and mechanisms that could explain the behaviour of human memory at the psychological level.[3] Hebb is mostly quoted for his views on the learning mechanism, the 'associativity' at the neural level resulting from strengthening of the coupling between cells that are simultaneously activated.[4] This, made explicit as a conjecture on synaptic plasticity,[5] has led to the experimental search for the 'Hebbian synapse', with the discovery of the strengthening (long-term potentiation, LTP) and weakening (long-term depression, LTD) of synapses, and of how these synaptic adaptations depend on pre- and post-synaptic activity.[6] On the theoretical side, a large amount of work has been done in order to understand if and how such learning dynamics can lead to learning associations. Efficient variants of the original Hebb proposal, such as the covariance rule and other closely related rules, in particular the so-called BCM rule, have been shown to be compatible with experimental data.[7] But Hebb did more than just suggest the existence of an adaptive mechanism modifying how neural cells interact. He made this proposal within a global analysis trying to explain human memory behaviour from the organisation and dynamics at the neural level. According to Hebb there are three key ingredients: large

neural assembly, high connectivity, and plasticity. First, a percept is supposed to be represented by the joint activity of a particular subset of neurons within a network composed of a large number of cells. This is already an important hypothesis, leading first to rate models: the information on a particular object is supposed to be simply given by the list of cells which should be activated (and those which should not be activated) when the object is evoked. Second, this particular pattern of activated/non-activated neurons is supposed to be dynamically stable thanks to the learning mechanisms: strong synapses will exist between cells which should both be active in a given pattern. This same mechanism is responsible for the associativity property: if only a proportion of the neurons are activated which should be active in order to evoke a particular object, then strong synapses will contribute to the activation of other neurons, leading to the activation of the full pattern. Connectivity must be high, in order to have recovery of the full information from the activation of almost any (large enough) subset of the coding assembly.

Attractor neural networks

Modelling memory started in the late 1960s,[8] but it is the physicist John J. Hopfield who proposed in 1982 the most direct mathematical formalisation of Hebb's ideas, with a model of interconnected 'formal neurons'. Simple in its formulation – too simple from the biological standpoint – the model remains complex from the mathematical point of view. Its full analysis has been made possible thanks to advances in the mid-1980s in the statistical physical theory of 'disordered systems', that is of strongly heterogeneous systems.[9] The analysis allows an understanding of why and under what conditions Hebb's original ideas are indeed sufficient to account for the behaviour of associative memory, and allows us to go far beyond Hebb's qualitative argument.[10] Besides this particular model, in his 1982 paper Hopfield introduced the general notion of attractor neural networks, in which the behaviour of an associative memory is generically observed.[11]

Many variants of the original Hopfield model have since been studied, with in particular the use of more complex models of neurons in order to allow for direct comparison with neurophysiology – mainly with the phenomenology of recordings in monkeys during memory tasks. The common property of these attractor neural networks is their formation during learning of 'memory states'. A given stimulus, when shown to the neural network, elicits a specific configuration of activity, which is then learned via Hebbian synaptic modifications (the Hopfield model uses in particular a covariance rule). These synaptic modifications in turn enable the neural assembly to sustain an active representation of the stimulus (i.e. the ensemble of neural activities specific to it) in its absence, in other words a 'memory state'.

From models to psychology and neurophysiology

Short-term memory models obtained as simple variants of the original Hopfield model allow for comparison with psychological data.[12] These models reproduce basic properties of human working memory as studied by psychologists – forgetting of old memories which are progressively erased by new ones, but also more elaborate phenomena such as primacy effects and proactive interference.[13] It is not clear, however, whether such models can account for more complex phenomena as described for example by Alan Baddeley or Jacques Ninio.[14] Another successful domain is the modelling of the effect of lesions in the

cortex. In particular, a phenomenon similar to prosopagnosia is generically observed in neural networks:[15] information related to individual memories is lost before the information which characterises the class. In addition, when learning a class of objects, a prototype of the class emerges as a memory state which has strong correlations with any one of the elements of the class, but which itself has never been learned.

It has been established how to build variant models incorporating enough biophysical detail to allow for comparison with electrophysiological data,[16] yet preserving the (relative) mathematical simplicity which is needed for performing the formal analysis of the model. In this new generation of attractor neural network models the role of inhibition is better understood: owing to strong recurrent inhibition, in each memory state only a small subset of neurons fires at more elevated frequencies, and, in the absence of external stimulation, the network stabilises in a state of low spontaneous activity – a property that cannot be obtained with the simpler models.[17] Realistic spiking patterns of activity are obtained with the 'integrate-and-fire' neuron (for which one describes the dynamics of dendritic integration of incoming synaptic inputs). The self-sustaining selective neural activity exhibited in these models is then in good correspondence with the phenomenology of recordings in monkeys during delayed response tasks, for example in the inferior temporal cortex or the prefrontal cortex.[18] The ability of these models to analyse experimental data and to make new predictions[19] has made possible new collaborations between physicists and neurobiologists, such as in Israel between the groups of D. J. Amit and of Hochstein and Yakovlev.

What do we learn from attractor neural networks?

In the models discussed above, memory retrieval is based on the dynamics of a large number of cells. Starting from some initial state (imposed by a stimulus), the network evolves towards an 'attractor' of the dynamics. In the simplest, deterministic, case, this attractor is a fixed point, which gives the response of the network to the stimulus: the stimulus is 'recognised' as being the object whose neural code is the set of active neurons in this fixed point. In more realistic cases where noise and/or spiking of cells is taken into account, the attractor is a stationary state, in which each cell has a mean activity which is constant in time. To have memory states as attractors of a dynamical system is already important, since it implies the associative property (the set of stimuli/initial conditions which lead to the same attractor is called the attractor's basin of attraction). It also gives a kind of semantic status to a memory state: the stability of the attractor gives a very special property to neural activity. What is significant for the system here is not just the list of cells which are activated, but in addition the dynamic stability (any small perturbation results in the system converging back to this state): the whole is more than the sum of its parts.

In the presence of noise, the very existence of memory states is an example of a collective phenomenon. Such states cannot exist with a small number of neurons, and here the intuition of Hebb, who insisted on the necessity for a large number of cells, is remarkable. For any system composed of a finite number of units, in the presence of noise the stationary state cannot be specific to any stimulus: the noise makes the network activity wander and thus lose any memory of the initial state – this is called 'ergodicity'. It is only in the formal limit of an infinite number of units that ergodicity can be broken, that is that several different attractors can exist. For finite but very large networks, the

behaviour of the network will look like that of an infinite system over a time which increases exponentially with the number of cells.

Finally there are the questions of retrieval quality and of capacity. In these models an object is considered as correctly memorised if learning succeeded in imposing an attractor in which the set of activated neurons corresponds as much as possible to the given set coding for the object. What is the maximal number of objects that can be put into memory? Here again the asymptotic limit of large systems is important. It is only in this limit that this 'as much as possible' can be quantified and given a clear meaning: either an object is well recognised, or it is not. Hence, for instance, at a given noise level there exists a maximal number of objects which can be well memorised. This number is typically proportional to the connectivity of the network (that is the number of cells from which a neuron receives synaptic inputs). This 'critical capacity' can be computed for many variants of the Hopfield model, in particular for variants of the Hebb learning rule. In the late 1980s, a new theoretical approach[20] led to the study of the optimal and typical (generic) properties of neural networks. It was then possible to compare the performances of a given model with the best possible ones. An unexpected and interesting result was that, in the limit of very low firing rates (that is in the limit when a given memory state activates a very low fraction of neurons), a simple Hebbian learning rule reaches the theoretical maximal storage capacity.[21] In addition, near to optimal performance is reached with the Hebbian rule proposed in the 1960s by Willshaw *et al.*, where synaptic efficacies can take only two values.[22] This is an important result since neurophysiological experiments indicate that indeed only a very low fraction (of the order of one per cent) of neurons participate in a given memory state.

COLLECTIVE OSCILLATIONS

In 1665, Christiaan Huygens described his discovery of an 'odd kind of sympathy' between the pendulums of two clocks, 'falling into synchrony' if hung together. This is the earliest known reference to the entrainment ('mode-locking') of two oscillators. Since then, it has become well known that even weakly coupled oscillators may have a tendency to become synchronised. Since individual neurons can behave as oscillators, it is not surprising that synchronised oscillations of neural activities are being observed – maybe one should rather ask how the brain avoids being permanently in a globally synchronised oscillatory regime! Oscillations are found in many parts of the brain, and different kinds of oscillations have been documented.[23] In particular, fast global oscillations in the gamma frequency range (that is of order 30 Hertz or more) have been reported in the visual cortex, in the hippocampus, and in the olfactory cortex.[24] Much faster oscillations still (200 Hertz) are known to occur in the rat hippocampus.[25]

On this topic, using analytical and/or numerical tools, most modelling studies of networks of neurons have focused on synchronised oscillations in regimes in which neurons behave themselves as oscillators.[26] In such cases, the distribution of interspike intervals is typically strongly peaked around the average value: the global (oscillating) activity of the network is well represented by the typical behaviour of a single cell in the network. Among the important outcomes of these studies is the attainment, in the case of globally coupled networks, of a regime where the network breaks into a small number of fully synchronised clusters.[27]

However, there are some less expected experimental data where individual neuron recordings show irregular spike emission, at a rate that is low compared to the global oscillation frequency.[28] Some numerical simulations of networks with detailed biophysical characteristics have exhibited properties similar to these experimental findings.[29] However, the biophysical complexity of individual neurons in these models makes it difficult to understand the origin of the phenomenon. This is an archetypal situation where theoretical analyses can help in understanding non-intuitive findings, and where the notion of collective state is particularly relevant. Brunel and Hakim have addressed the issue of the possible appearance of fast oscillations in a network where (non-oscillating) neurons fire irregularly with an average frequency that is much lower than the population frequency.[30]

Contrary to untrained intuition, it is inhibition and not excitation which appears to be the key ingredient. It was already known that recurrent inhibition plays an important role in the generation of synchronised oscillations, as shown in both in vivo[31] and in vitro[32] experiments in different systems. This has been confirmed by several modelling studies.[33] On the other hand it has also been shown generically that networks in which inhibition balances excitation have neurons with irregular and low firing.[34] Simulations with sparsely connected 'integrate-and-fire' neurons have shown that the highly irregular activity at the single neuron level can be accompanied by damped fast oscillations of the global activity.[35] In the first detailed theoretical analysis, the dynamics of a network of sparsely connected inhibitory 'integrate-and-fire' neurons has been studied analytically in a regime where individual neurons emit spikes irregularly and at a low rate. In the limit when the number of neurons is very large, the network exhibits a sharp transition between a stationary and an oscillatory global activity regime where neurons are weakly synchronised: the activity becomes oscillatory when the inhibitory feedback is strong enough. The period of the global oscillations is found to be mainly controlled by synaptic times but depends also on the characteristics of the external input.[36]

CONCLUSION

The current generation of memory models, based on the attractor neural network concept, can be confronted with experimental data from both psychology and neurophysiology. Composed of reasonably realistic elements, these models remain however simple enough to be analysed and simulated. Much research remains to be done, notably concerning the dynamical properties of such systems and the learning of spatiotemporal patterns. These models may help to produce a better understanding of specific systems (hippocampus, higher sensory cortices, prefrontal cortex), but also of the interactions between systems, for example the cortico-hippocampal interactions. A major challenge is to understand how the sensory systems build efficient representations to be stored in memory: despite important progress made in the analysis of sensory coding,[37] only few attempts have been made to combine the coding and storage stages.

Starting with a function (memory) and its properties (forgetting, associative behaviour), it has been shown by modelling how this function can be seen as emerging from the collective properties of networks of interconnected neurons. In the case of fast oscillations, the modelling has allowed the observed collective behaviour to be explained, yet without providing an idea of function: the role of these oscillations remains unclear, despite several

proposals, among which the most popular is that oscillations would be useful for putting into correspondence different neuronal populations. More experiments are clearly needed here in order to make progress on the theoretical side.

NOTES

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