Investigation of sequence processing: A cognitive and computational neuroscience perspective

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Serial order processing or sequence processing underlies many human activities such as speech, language, skill learning, planning, problem-solving, etc. Investigating the neural bases of sequence processing enables us to understand serial order in cognition and also helps in building intelligent devices. In this article, we review various cognitive issues related to sequence processing with examples. Experimental results that give evidence for the involvement of various brain areas will be described. Finally, a theoretical approach based on statistical models and reinforcement learning paradigm is presented. These theoretical ideas are useful for studying sequence learning in a principled way. This article also suggests a two-way process diagram integrating experimentation (cognitive neuroscience) and theory/computational modelling (computational neuroscience). This integrated framework is useful not only in the present study of serial order, but also for understanding many cognitive processes.

Keywords: Cognitive science, computational modelling, reinforcement learning, serial order, sequence learning.

'. . . the coordination of leg movements in insects, the song of birds, the control of trotting and pacing in a gaited horse, the rat running the maze, the architect designing a house, the carpenter sawing a board present a problem of sequences of action . . .'.

— Karl Lashley[1]

SERIAL order in behaviour has been studied for a long time. Serial order processing or sequence processing is a key issue in many areas of cognitive science such as auditory perception, visual perception (three-dimensional object recognition), speech perception, language, skilled behaviour, goal-directed planning, and problem-solving. The role of serial order in cognition can be investigated using a two-pronged approach. First, an experimental approach can be adopted that reveals brain areas (neural bases) involved and their interactions while human or animal subjects are engaged in tasks such as pressing buttons in a particular order, operating a lever in a specified sequence, etc. that require sequence processing. Such experimental investigation strategies form the core of cognitive neuroscience. Secondly, a modelling approach can be adopted that enables mathematical and computational formalization of the dynamics of brain activation observed through experiments. Modelling and simulation methods form the core of computational neuroscience. It is expected that computational neuroscience efforts would eventually pave the way for building intelligent devices.

Before enumerating the issues related to sequence processing, serial and parallel aspects of cognition are clarified by taking face perception as an example. Recognizing a face appears to involve parallel processing, whereby various features of the face are apprehended simultaneously and recognition ensues from the parallel operations. However, experimental evidence suggests that face perception involves serial processing. Yarbus[2], in a classic experiment, monitored subjects' eye movements as they viewed portraits. Subjects reported apprehending the portrait as a whole, but their eye movements revealed a different phenomenon. During the process of perceiving the face, observer's attention moved from one point of fixation to another. By analysing the distribution of points of fixation, the duration of fixation and the distinctive cyclic pattern of examination, Yarbus concluded that the subjects made saccadic eye movements, fixating successively at the most informative parts of the image. Thus these observations point out that underlying an apparently parallel process of face perception, there is a serial oculomotor process. This example is presented to clarify the meaning of serial and parallel processes and also to point out that many cognitive phenomena have both the aspects.

In this article, we take serial order in cognition as an example to illustrate how a cognitive phenomenon can be investigated in a multidisciplinary fashion. Experimental investigation of various aspects of serial order such as perception, learning, representation, organization, neural bases comprises the cognitive neuroscience perspective. We propose a theoretical modelling approach, wherein Markov models and reinforcement learning are combined in order to understand sequence processing from the computational neuroscience perspective. Finally, we advocate an integrated framework that combines experimentation

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and computational modelling to enable holistic investigation of a cognitive phenomenon.

Issues related to serial order

In the following sections, a detailed discussion of several issues related to serial order is presented. The issues discussed are the origin of sequential behaviour in humans, possible representation schemes available, the organization of sequences, the order and timing of individual elements of a sequence, learning modes, stages and strategies applicable for sequence learning and the issues in sequence perception. It is to be noted that no single paradigm covers all the issues in a unified fashion. Therefore, we discuss each of these issues with the help of a representative example.

Origins of sequential behaviour

There are broadly two classes of origin for sequential behaviour – one is evolutionary and the other is through learning. A variety of natural sequential patterns or ritualistic behaviours can be seen in many species, including humans. Some examples are the grooming movements in rats, locomotion, mastication, rhythmic respiratory movements, etc. Many species apart from humans are also capable of acquiring sequential behaviours via instrumental conditioning. In the following, we give one example of pre-wired behaviour (grooming) and two examples for learned behaviour (working memory, imitation).

Berridge and Whishaw[3] have studied ritualistic grooming movements in rats. They demonstrated a crucial role for the neostriatum in exhibiting species-specific (genetic or pre-wired) sequencing behaviours in rats. On the other hand, examples of learned (adaptive) behaviour include speech, language, skills, etc. We now present examples of sequential nature in adaptive behaviours, such as working memory and imitation learning.

Working memory tasks involve linking events across time and are also essential for goal-directed behaviour. An important component in serial order in behaviour is the ability to hold information on-line, and being able to sequence behaviours in order to attain the desired goal. Diamond[4] studied performance of infants and monkeys on delayed response tasks that assess the working memory capacity. These tasks require subjects to hold information for a length of time in the mind, even in the absence of external cue. The subject initially watches the experimenter hide a desired object in one of two identical wells. After a brief delay, during which the wells are hidden from view, the subject is allowed to reach out and retrieve the hidden object. Infants of 7.5–9 months fail delayed response under the same conditions and in the same way, as do monkeys with lesions of the dorsolateral prefrontal cortex. It is therefore suggested that improved performance on this task is an index of maturation of frontal cortex function. Diamond[4] proposed that maturation of the prefrontal cortex might make possible the age-related developmental progression of human infants on working memory tasks. The working memory studies described above give clues to the adaptive origin of some behavioural sequences.

Certain types of adaptive behaviour such as imitation also involve serial order. It has also been proposed that propensity to engage in complex sequential activities such as imitation is a precursor to high-level behaviours such as empathy and mental simulation[5]. This kind of imitation-based learning is a useful adaptive behaviour and is being increasingly used for training robots. Schaal[6] demonstrated that imitation learning offers a promising route to gain new insights into mechanisms of perceptual motor control that could ultimately lead to the creation of autonomous humanoid robots.

Thus, some behavioural sequences have pre-wired origin, while many more are learned.

Representation of sequences

In the following we present evidence for both distributed and local representation of human movements. Georgopoulos *et al.*[7] have shown that reaching movements of the arm are represented not by single neurons, but by the combined activity of a large population of cells in the motor cortex of the brain. These researchers recorded 568 cells in monkey cortex, while it performed reaching arm movements. They found that each individual cell responded best for arm movements in a given direction, and its response gradually tailed-off for arm movements in adjacent directions. They argued that the direction of movement is represented in the motor cortex by a population vector, which rotated when the monkey intended to move a lever in a rotated direction, prior to movement. This experiment illustrates the distributed nature of representation for elemental movements in the motor cortex. Recent studies by Lu and Ashe[8] suggest that apart from elemental movements, sequential movements also have distributed representation.

On the other hand, there is experimental evidence supporting local representation of sequence of movements. Tanji and Shima[9] have found a group of cells in the cerebral cortex of monkeys whose activity is exclusively related to a sequence of movements performed in a particular order. Two monkeys were trained to perform three movements (push, pull or turn a manipulandum) in four different orders. Before each movement, monkeys waited for a tone that served as a movement trigger. During learning phase, the correct movement was indicated by a green (push), yellow (pull) or red (turn) light. After five learning trials, the monkeys performed the sequence from internal memory in the absence of external visual cues. It was observed that the cells in the supplementary motor area (SMA) were active while the animal was waiting to perform a motor sequence of turn–pull–push. But such activity was not observed while the monkey was waiting to perform a different sequence of turn–push–pull for which a different set of cells was activated.

In summary, while studies by Georgopoulos *et al.*[7], and Lu and Ashe[8] indicated a distributed representation for individual arm movements, studies by Tanji and Shima[9] suggested a possible local representation for sequences of movements.

Organization of sequences

Internal organization of behavioural sequences can be either linear (flat) or nonlinear (hierarchical) (Figure 1). Lashley[1] argued that the sequential responses that appear to be organized in linear and flat fashion concealed an underlying hierarchical structure. Hierarchical representations of sequences have an edge over linear representations. They allow easier access to common subroutines of sequences, easier to self-repair in the event of failure, and combine efficient local action at low hierarchical levels while maintaining the guidance of an overall structure. A linear (flat) organization of a sequence will be in the form of one long linear string of actions, as shown in Figure 1. While the representation is simple from storage point of view, there can be potential problems during retrieval. For instance, if the nth element has to be retrieved, all the $n - 1$ preceding elements have to be processed. Further, if there is a break in the chain, subsequent elements will become inaccessible. On the other hand, a hierarchical representation would have multiple levels of representation. Figure 1 shows a two-level hierarchical representation. At the lower level, representation of the elements of the sequence is flat. At the higher level, control nodes (chunk nodes) are connected among themselves in a linear fashion and also connect to their respective sequence elements forming a hierarchy. A break in the link between lower level nodes does not render any part of the sequence inaccessible, since the control nodes (chunk nodes) would still be able to facilitate access to the lower level nodes.

In human behaviour, hierarchical structuring has been argued to be essential for many acquired skills, such as language, problem-solving and everyday planning[10–13]. Further, studies show that representation at the higher level supports grouping of low-level units to form what are popularly known as chunks[14–19]. Chunking also enables overcoming the limitations imposed by limited-capacity working memory, whose limit is proposed to be 7 ± 2 constituents[20]. In summary, strength of the evidence from experimental and theoretical studies so far points to a hierarchical representation.

Encoding of serial order

The order of encoding of sequence of entities into long-term memory is another issue to be considered in serial order. The items could be stored in the order they are encountered, i.e. the first items are stored with more emphasis than the last items or the other way round. If the first items are stored more strongly and recalled more easily, then the process is said to have *primacy* effect. On the other hand, if the last items are emphasized more and retrieved with ease, then the process is said to possess *recency* effect. Figure 2 shows a serial learning curve that is typically seen in list learning tasks. This curve reveals that subjects recall words presented at the beginning and the end of a list, better than words presented in the middle. Items at the beginning may take advantage of the long-term memory laid down by more frequent rehearsals. Items at the end are easy to recall because they are active in working/short-term memory[21]. Any study of serial order has to address the primacy and recency issues.

Timing-related issues

Apart from issues related to representation, organization and order of sequences, the timing of individual units in a sequence is also an important factor. For example, in poetry, if the relative timing is not maintained, the rhythm is lost.

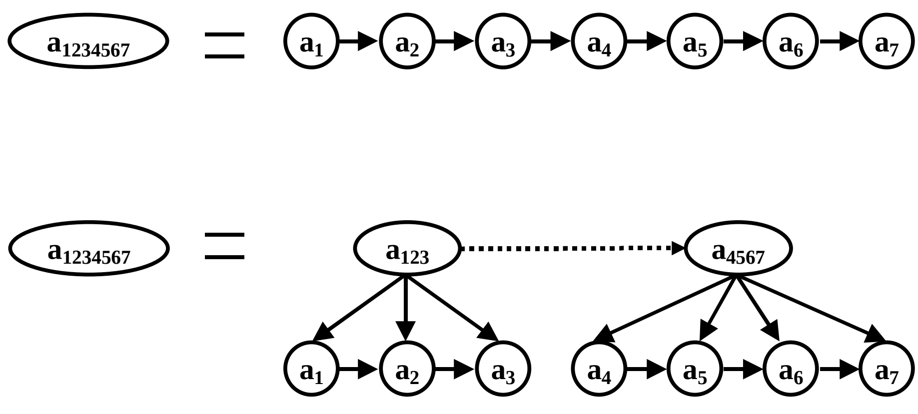

Figure 1. Flat versus hierarchical representation. Schematic diagram depicts a sequence of seven elements represented in flat (linear) and hierarchical (nonlinear) arrangement. In hierarchical organization, nodes a_{123} and a_{4567} represent chunks of elements.

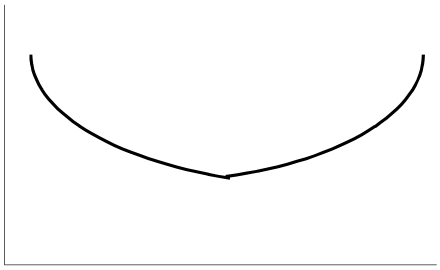

Figure 2. Serial position curve showing the relationship between the list position of an item and associated probability of recall. The first half of the curve where the first few elements have higher recall probability depicts the primacy effect. In the second half, the last few items have higher probability of recall, pointing to the recency effect in serial list learning.

On the other hand, it has minimal effect in prose-like text. There are three attributes for timing, namely execution time of each individual unit in a sequence, time delay between two consecutive units, and overall time taken for sequence execution. The first two attributes can be either fixed throughout the entire sequence or variable. The variations could possibly depend on the context of occurrence of each individual unit in the sequence. Thus timing and temporal modulation issues are important for deeper investigation of sequence processing. In a recent review, Janata and Grafton[22] suggested three important subcomponents related to understanding neural basis of serial order in music. They are timing, attention and sequence learning. Janata and Grafton[22] argued that studying aspects of music would lead to better understanding of complex human behaviours.

Learning of sequences

In this section, we will discuss different aspects related to learning, such as implicit and explicit learning modes, stages in learning, and learning strategies.

Learning modes: Learning of serial order may be operating in one of the two modes – explicit learning mode or implicit learning mode. Explicit learning includes conscious attempts to construct a representation of the task; directed search of memory for similar or analogous task-relevant information, and conscious attempts to derive and test hypotheses related to the structure of the task[23]. This type of learning has been distinguished from alternative modes of learning, termed implicit learning, in which task-relevant information is acquired automatically and without conscious awareness of what is being learnt. An example of implicit learning task is SRT (serial reaction time) task, where the subjects execute sequential finger movements in response to visual cues that appear one after another. Unknown to the subjects, a repeating sequence is embedded among the random sequence of cues. Although subjects do not become aware of the repeating sequence, they exhibit improved response times during the execution of the recurring sequence compared to the random ones. The improved response times are attributed to implicit learning. It has been found that distinct brain areas are involved in implicit and explicit learning modes[24].

Learning stages: It is a common observation that when a skill, involving sequence of entities, is being acquired, we need to be more attentive in the initial phase; however, during the later, more automatic phase, attention can be engaged in other tasks. Fitts[25] proposed a framework for skill acquisition that included two major stages in the development of a cognitive skill: a declarative stage in which facts about the skill domain are interpreted and a procedural stage in which the domain knowledge is directly embodied in procedures for performing the skill. Brain activation differences were also observed when subjects learned a sequential skill and progressed from the early, more deliberate and attentive stage to the late and more automatic stage[26–28].

Learning strategies: We can distinguish learning strategies broadly into two main categories: supervised and unsupervised, based on whether evaluative feedback was provided or not. Feedback signal provides an assessment of the performance of the system during the learning process. In supervised learning, we assume that the teacher provides the desired response at each instant of time that can be used to calculate the errors and make appropriate corrections in order to eventually achieve the desired target. In a variation of supervised learning called reinforcement learning, a coarse feedback indicating the quality of the output is provided without specifying the desired response itself. In unsupervised learning, the desired response is not known. Thus explicit error information cannot be used to improve behaviour in unsupervised learning. The system needs to discover the inherent regularities present in the inputs and self-organize the information. It has been proposed that a different set of brain areas is associated with different learning strategies[29]. Thus adaptive sequential behaviours could be acquired using any one of the strategies, i.e. supervised, reinforcement, or unsupervised learning.

Perception issues in sequence processing

A potential theory of serial order needs to deal with various sequence perception problems organized broadly into two categories: sequence recognition and sequence recall/generation. These problems can be stated formally as shown below[30,31].

(i) Recognition: Given a sequence $S_i, S_{i+1}, \ldots, S_k$, the recognition problem involves determining if the given sequence is legitimate or not.

$S_i, S_{i+1} \ldots, S_k \rightarrow$ Yes or No, where $1 \leq i \leq k \leq \infty$.

(ii) Recall/generation: Given a sequence $S_i, S_{i+1} \ldots, S_k$, recall or generation problem involves generating or recalling the next item S_{k+1}.

$S_i, S_{i+1} \ldots, S_k \rightarrow S_{k+1}$, where $1 \leq i \leq k \leq \infty$.

In both recognition and recall, an internal representation of sequence may be needed for making perceptual judgments and for prediction (or generation) of subsequent elements, respectively. Future experimental investigations would need to tease out differences in the cognitive processes involved and the concomitant differences in brain areas sub-serving recognition and recall/generation of sequences.

Brain areas sub-serving aspects of serial order

The current working assumption in neuroscience is that various functions are organized in a modular fashion in the brain. In this section, we shall first present a brief overview of various brain areas and their function.

The central nervous system is composed of the brain and the spinal cord. Stimuli from sensory/peripheral organs are carried via the spinal cord and processed in the brain. The corresponding motor signals (outputs) get transmitted to the appropriate peripheral system via the spinal cord. The brain is composed of three major components, namely the cerebrum, the cerebellum, and the sub-cortical areas. The brain is divided into two hemispheres called the left hemisphere (left lobe; Figure 3) and the right hemisphere (right lobe). These hemispheres have rich interconnections through the corpus callosum. A prominent groove on the surface of the cerebrum when viewed from the top and running from left to right, serves as a standard landmark called the central sulcus. The cortex anterior to the central sulcus is called the anterior (frontal) lobe and that which is posterior is called the posterior lobe. Anterior lobe comprises the prefrontal cortex, supplementary motor area, pre-motor area and the primary motor area. Posterior lobe comprises the sensory cortex, parietal cortex, occipital (visual) cortex and the temporal areas. Some of the prominent nuclei that lie below the cerebrum, i.e. in the sub-cortical region are the basal ganglia, the hippocampus and the amygdala.

The cerebellum is located below the cerebral cortex. The spinal cord connects the brain at the base near the medulla oblongata. In the remainder of the section, we describe results from our own and other experimental efforts investigating the brain areas associated with various aspects of serial order.

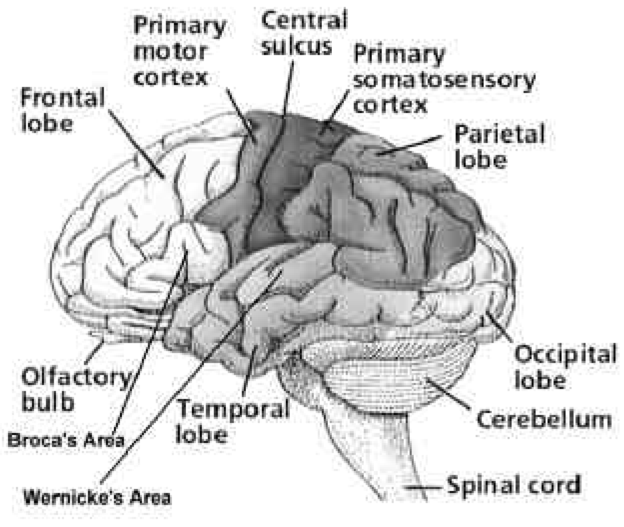

Figure 3. Generic brain areas. The four lobes of the brain (Image from Purves *et al.*, *Life: The Science of Biology*, 4th edn; used with permission from Sinauer Associates Inc., USA, 1999).

Brain areas involved in serial order

In this subsection we summarize some representative experimental findings corresponding to the issues related to serial order elucidated earlier.

Origins: The area specifically proposed for procedural memory (such as skills and habits) is the striatum[32]. Berridge and Whishaw[3] showed that lesions of the precentral cortical areas or of other neo-cortical areas did not affect the performance of ritualistic behavioural sequences in rats. On the other hand, lesions of the neostriatum, which receives inputs from the cerebral cortex, impaired the performance thereby implicating a role for the striatum in pre-wired behavioural sequences. Curran[24] and Clegg *et al.*[33] also summarized evidence for striatal involvement in sequence learning based on experiments involving implicit learning tasks such as the SRT.

Representation: Studies by Georgopoulos *et al.*[7] and Lu and Ashe[8] suggested a distributed representation for individual arm movements in the motor cortex of rhesus monkeys. On the other hand, Tanji and Shima[9] demonstrated experimental evidence supporting local representation of sequence of movements in the SMA of monkeys.

Organization and timing: Apart from the above findings, there are other studies that investigated neural bases responsible for the timing and chunking aspects in serial order. Timing aspects in sequence learning have been explored and the cerebellum is found to be critically involved[34,35]. Disruption of chunk representation of movement sequences in pre-SMA was demonstrated using transcranial magnetic stimulation study by Kennereley *et al.*[36]. The review of Janata and Grafton[22] suggested that the cerebellum, SMA, premotor cortex, basal ganglia and parietal cortices are involved in timing aspects of both perceptual and motor tasks. They pointed out that these areas might be playing an important role in perception–action cycle.

Learning: We pointed out earlier, the various aspects of sequence learning, namely learning modes, learning stages and learning strategies. Curran[24] described distinct brain areas involved in the implicit and explicit modes of sequence learning. He suggested involvement of striatum in the implicit learning mode and the medial, temporal and diencephalic brain regions during the explicit learning mode. Squire and Zola[32] also reported similar findings during implicit and explicit memory-related tasks.

Studies by Jupetner *et al.*[26,27] have shown that as learning progressed from controlled (new learning) stage to automatic stage in a finger movement learning task, brain activation shifted from the anterior to the posterior parts both in the neocortex and the sub-cortical structures. Sakai *et al.*[28] demonstrated transition of brain activity from the frontal regions (pre-SMA and dorsolateral prefrontal cortex) to the parietal regions (precuneus and lateral parietal cortex) as learning advanced from early to non-early (intermediate and late) stages respectively. Our behavioural[37] and functional magnetic resonance imaging experiments investigated different aspects of procedural memory such as representation[38], complexity[39] and learning mode[40]. We proposed possible cortical localization of various modules and mappings that subjects use while practising a set of finger movements in response to visual stimuli. In early stages of learning this task, subjects may follow a long route in which the response is mediated by a visuo-spatial mapping followed by a spatial-motor mapping. In the late stages of learning this task, subjects may follow a shorter route, where they utilize a direct visuo-motor mapping. Further, we hypothesized that there are two sequence representations, effector-independent in visual/spatial coordinates and effector-dependent representation in motor coordinates. Possible neural bases for the effector-independent sequence representation may be in the parietal–prefrontal network and effector-dependent representation may be in the SMA–primary motor cortical network. Basal ganglia structures may also be differentially involved in supporting different representations and the premotor cortex may mediate various mappings[37,38,41].

Doya[29,42] suggested that the cerebellum, basal ganglia, and cerebral cortex are specialized for different strategies of learning, namely supervised learning, reinforcement learning and unsupervised learning respectively.

Perception: In a recent investigation, Pasupathy and Miller[43] demonstrated that the learning-related activity in prefrontal cortex and striatum showed different time courses during associative learning. Their results on monkeys suggested that the striatum generates quick predictions about the behavioural choice and the prefrontal cortex reveals the slower accumulation of the correct answer.

Theoretical framework and computational modelling

So far, we had highlighted the cognitive neuroscience perspective of serial order in cognition. In this section a discussion is presented on how computational neuroscience efforts can be directed towards theoretical investigation of serial order. In the literature, several researchers described computational models for serial learning. These models can be broadly classified into three categories – biologically inspired models, connectionist models, and hybrid models. In biologically inspired computational models, some aspects of anatomical organization and function are mimicked[44,45]. In connectionist models, the aim is to mimic the overall behaviour of the biological system rather than replicating the internal organizational details[46]. In hybrid models, engineering principles enable the construction of models that illuminate biological function. These models usually do not attempt an explicit replication of anatomical organization[47,48].

In order to illustrate the typical activity taken up under the enterprise of computational modelling, we present here a theoretical framework for modelling sequence processing focusing on the organizational aspects. The framework we propose here falls under the third category, i.e. hybrid computational model. We propose a two-level model where Markov models and reinforcement learning are combined to specifically address how biological systems learn to organize sequential information in a hierarchical fashion.

Curran[24] summarized results from the implicit learning studies and concluded that in sequence learning tasks, basal ganglia systems may enable extraction of first-order sequential dependencies and that cortical–basal ganglia loops may be responsible for learning higher order structures. Based on this empirical evidence we propose a two-level model where at the lower level, first-order sequential dependencies are extracted and at the higher level, hierarchical structure corresponding to the entire sequence is captured using reinforcement learning.

First-order Markov model

Markov model is a well-formulated mathematical framework for capturing first and higher order sequential dependencies among random variables describing the behaviour of a system. The main assumption (also called Markov assumption) is that prediction of the next state depends only on a portion of the previous history of state transitions. In the case of first-order Markov models, the probability that q_t (state at time t) is equal to i is completely predictable by knowing q_{t-1} and ignoring the rest of the previous state history (a second-order Markov model would require q_{t-1} and q_{t-2} to predict q_t). A formal definition of the first-order Markov model is given below.

$$P(q_i = i|q_{t-1} = j,\, q_{t-2} = k, \ldots) = P(q_t = i|q_{t-1} = j).$$

Reinforcement learning

Reinforcement learning (RL) has been proposed as a biologically realistic framework for learning sequential decisions in animals and humans[49]. In this paradigm, the sequential decision problem involves assuming a policy (a mapping from the states to possible actions) and learning a value function over the state space, so that the sequence of actions maximizes the expected future reward. The most popular method for learning the value function is the method of temporal difference (TD). A formal definition is given below.

$$V(t) = E[r(t+1) + r(t+2) + \mathbf{L}],$$

$$d(t) = r(t) + V(t) - V(t-1),$$

where $V(t)$ represents the value of a state, $r(t)$ is the reward and $d(t)$ is the temporal difference signal all at time t. $E[.]$ represents the expectation or averaging operator. Value of a state, $V(t)$, is set to be the average future reward that is likely to be obtained in the current state. Temporal difference signal, $d(t)$, tracks the difference between the expected reward and actual reward and serves as the reinforcement learning (internal feedback) signal.

First-order Markov models alone would capture a flat organization of the sequence and do not incorporate learning. Although RL models incorporate learning, the policies that are learned would still have a flat organization. We propose that by combining these two models and utilizing the TD error signal, hierarchical policies could be learned. Computer modelling (simulation) of the two-level architecture (Figure 4) combining Markov models and RL is expected to reveal whether models based on this framework can really solve the hierarchical sequence decision problems. Such models would mimic the hierarchical nature of organization of sequences as observed in biological systems, without an explicit replication of the anatomical organization within.

As already pointed out earlier, a unified framework for addressing various aspects of serial order has not been attempted either for designing cognitive neuroscience experiments or for constructing computational models. This still remains an open problem.

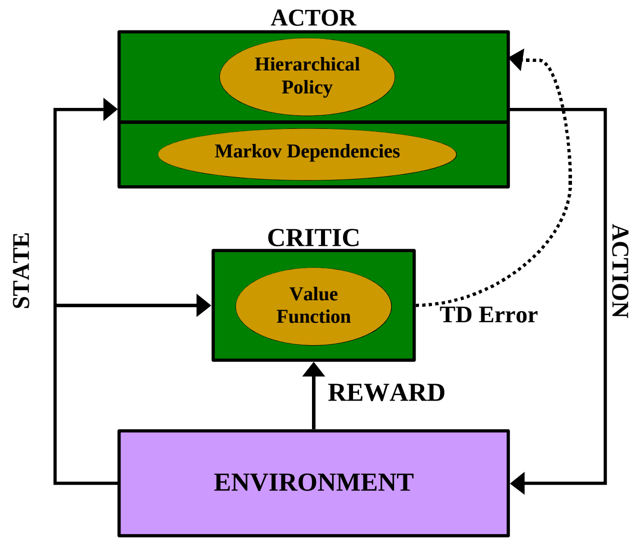

Figure 4. Block diagram of the proposed hybrid model. Actor–critic based model incorporating Markov model and hierarchical policy as sub-modules in the actor module. The two levels in the actor module, namely the Markov model and the hierarchical policy module would enable learning hierarchical sequence decision problems.

Conclusion and future work

Sequencing is an essential aspect of animal and human behaviour. An introduction to serial order, an essential aspect of human behaviour, is given. A brief summary of various aspects of serial order is presented here. The issues discussed are the origin, representation schemes, organization, order, timing, learning and perception. Brain areas related to sequencing are summarized and our own empirical efforts in this direction are also described. A theoretical framework combining the mathematical ideas of Markov models and RL is proposed as an example for computational modelling of hierarchical sequences. There is an urgent need to formulate unified framework for investigation of serial order from cognitive neuroscience and computational neuroscience perspectives.

There is also an immediate need to facilitate a bridge between the cognitive and computational neuroscience streams. Figure 5 depicts an integration of the efforts involved in understanding serial order or sequencing. There are two main efforts in this direction – one is experimentation (cognitive neuroscience) and the other is building theoretical framework and undertaking computational modelling work (computational neuroscience). The former

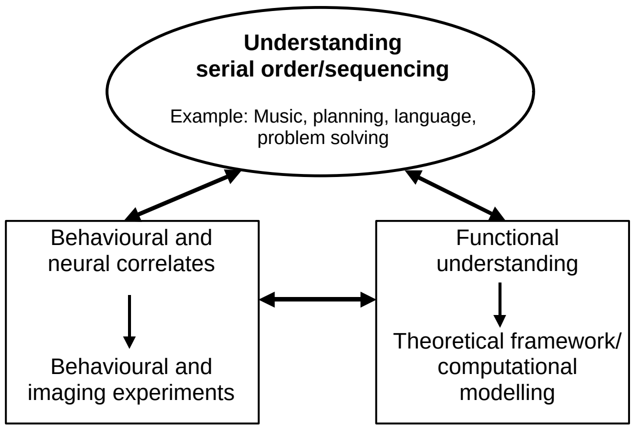

Figure 5. Block diagram depicting scientific endeavour. Relationship between experimentation (cognitive neuroscience) and modelling (computational neuroscience) is emphasized in promoting holistic understanding of serial order.

effort enables understanding of the behavioural and neural correlates of sequencing. The latter effort engenders functional understanding. It is difficult, if not impossible, to gain the complete functional understanding of a cognitive phenomenon by a pure empirical approach. Similarly, a pure theoretical or modelling approach will run the risk of lacking the biological realism and relevance. Hence, the empirical and modelling efforts are of utmost importance and they reinforce each other. The other point emphasized here is that these efforts must go hand-in-hand. The modelling exercise may also spawn further predictions to be experimentally verified in future. Although the current article has focused on sequence learning, the proposed integration would serve as an indispensable model for organizing scientific endeavours toward understanding any cognitive phenomenon.

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