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Predicting and binding: interacting algorithms supporting the consolidation of sequential motor skills

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The efficient execution of serially ordered actions is crucial for many everyday tasks. Rather than emerge from a singular learning process, a growing body of evidence in both cognitive science and neuroscience suggests that the acquisition of habitual motor sequences relies on a multitude of learning systems that fall under two general classes of computation: fast prediction of transition probabilities between events and slower binding of serial actions into unified sets. Here we review the emerging empirical support for this multi-system model of sequential skill acquisition and show how these systems coordinate together to foster the crystallization of complex skills across time.

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Introduction

Many everyday behaviors are predicated on our ability to effortlessly produce complex, serially ordered actions. For example, typing the word 'brain' on a keyboard requires serially pressing the 'b', 'r', 'a', 'i', and 'n' keys as quickly and accurately as possible. Novices execute each key press slowly, planning each successive movement independently. By contrast, experts can perform the same series of keystrokes in rapid succession, executed as a fluid, unified action. This ability to execute a unified set of serially ordered actions represents one example of a more general form of skill learning known as sensorimotor sequence learning.

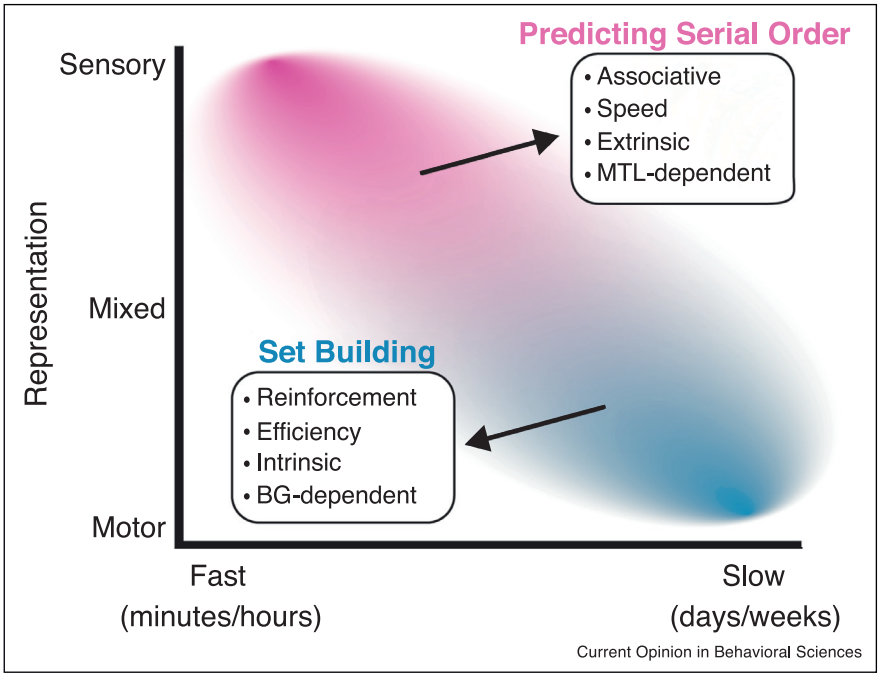
Sensorimotor sequence learning has fascinated cognitive science for over sixty years [1] and is thought to play a central role in a wide range of intelligent behaviors, including language learning (see [2] for review). While initial research sought to characterize this form of learning as a singular process [3] or as a single learning system operating at different representational levels [4], overwhelming evidence now supports the hypothesis that the consolidation of sequential motor skills relies on multiple interacting systems that learn different parts of the serial ordering problem at different timescales. Here we show how these systems can be segregated into two general categories of learning processes, based on the computational goals they serve: fast prediction of serial ordered events and slow binding of responses into sets of unified actions (Figure 1). These two interacting computational mechanisms operate along a learning continuum, between sensory and motor levels, working together to sculpt behaviors over time so as to maximize the complexity of produced actions while minimizing the computational costs of planning and executing them.

Predicting serial orders of events

Early in learning, a novice typer will show faster and more accurate responses to frequently paired serial actions than to infrequently paired actions. For example, repeatedly typing the word 'brain' leads to faster 'r' key presses when they follow a 'b' key press, but pressing the 'r' key would be slower if the preceding letter was something unusual, such as 'q'. In this way, the brain associatively learns the transition probabilities between sequential stimulus-response events over the course of only a few minutes of practice [3,5]. When studied in the context of language development, this same process is known as statistical learning [6]. Classically, statistical learning refers to the phenomenon whereby neural and behavioral responses become more efficient to serially repeated sensory events than to unexpected events. This learning happens very quickly and can be detected within the course of a single training session (for a review of statistical learning, see [7]). In this way, over the course of several minutes of repeated exposure, the brain learns to estimate the conditional probability of an upcoming sensorimotor plan, X_{t+1}, given the immediately preceding plans, $P(X_{t+1}|X_{t-1}, \ldots, X_{t-n})$, to make faster and more accurate responses.

This predictive process is evident in very early sensory processing [8,9]. For example, neurons in the inferotemporal cortex (IT), a visual processing area, learn to modulate their responses to serially presented visual stimuli

Figure 1



Continuum of sensorimotor sequence learning. Schematic of the temporal and representational spaces occupied by processes that learn to predict transition probabilities between serially ordered events (magenta) and processes that learn to bind actions together into unified sets (blue). Insets indicate summary features of each learning process that are described in detail in text. *Abbreviations*: MTL, medial temporal lobe; BG, basal ganglia.

depending on the transition probability between cues [10]. Yet IT neurons do not simply track the co-occurrence of stimuli, but also appear to track the conditional probabilities of events, as their activity is attenuated when the conditional probabilities are modified [11•]. Of course, learning transition probabilities may not be restricted to predicting sensory cues. For example, in a classic study, Mushiake and colleagues showed that cells in the macaque dorsal premotor cortex (PMd) were tuned to the transition probability between sequentially cued movements [12], suggesting that motor systems also track the transitions between serial actions. Although given the extensive training required to get the animals to learn the task, this may reflect a probabilistic variant of chunking, rather than true statistical learning (see next section).

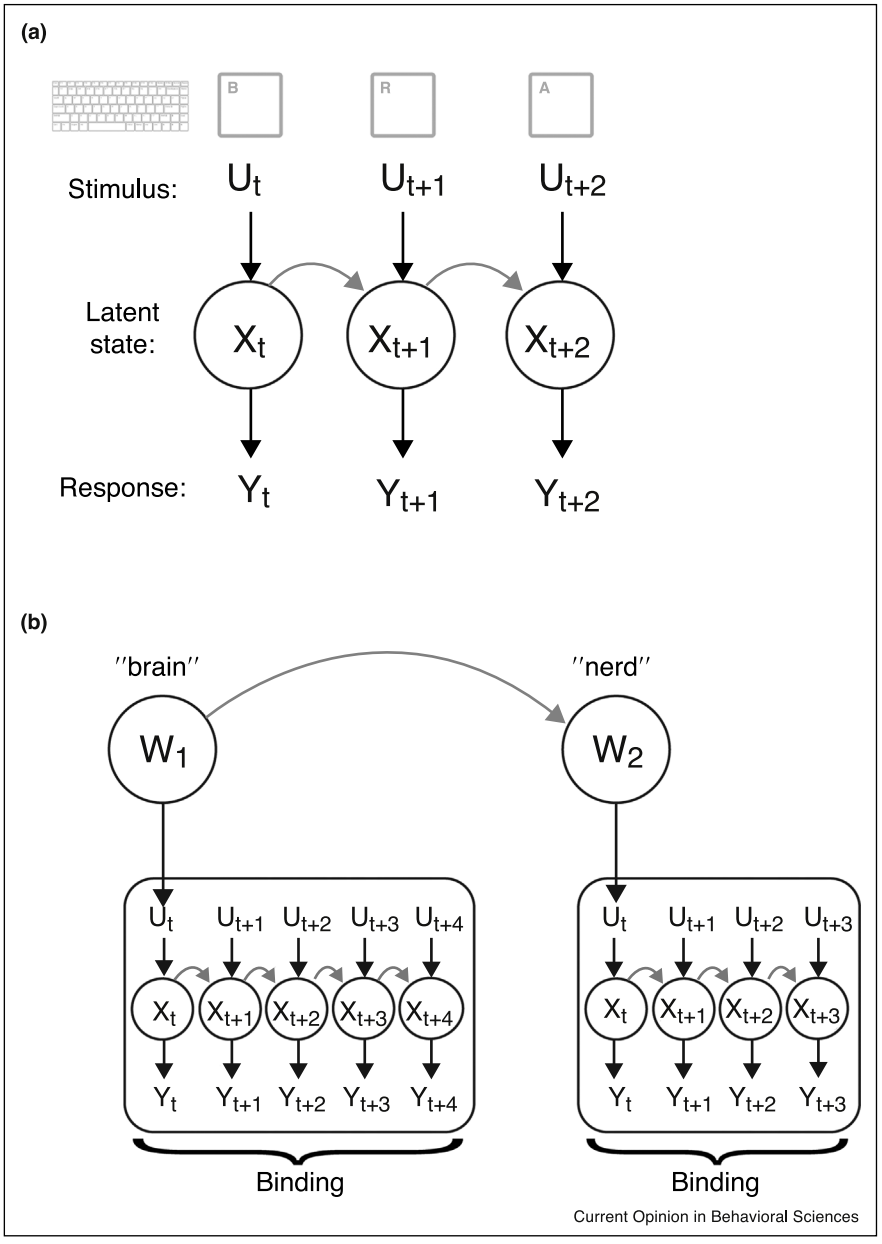
Mechanistically, recent evidence suggests that this fast detection of serial ordering may rely, at least in part, on the medial temporal lobe, particularly the hippocampus [13–19]. A sub-population of hippocampal cells shows tuning for the temporal associations between sequences of events [20–22], suggesting that the hippocampus may track serial probabilities and bias cortical sensory and motor processing via top-down signals. This hypothesis is bolstered by several other lines of evidence. For example, the consolidation of complex response sequences is improved following a normal sleep cycle [16,23–25], a classic signature of hippocampal-dependent learning. Co-activation of hippocampal and striatal networks is observed during sequence learning [26,27], particularly when learning the temporal structure of sequential events [28]. Finally, patients with damage to the hippocampus show impairments in single-session sensorimotor sequence learning [29,30], particularly during the initial acquisition phases of learning when declarative mechanisms are crucial for picking up transition probabilities between stimuli [31].

Taken together, the emerging evidence suggests that fast associative mechanisms learn first-order transition probabilities between both sensory cues and actions early in learning (see also [32•]). This ability to reliably predict upcoming events speeds up the ability to resolve a stimulus-response mapping and thus results in faster responses, likely through adjusting the threshold for evidence needed to initiate a response (for review see [33]).

Binding sets of actions

Relying solely on learning first order transition probabilities limits the capacity of producing complex sequential actions. This is because the number of events, n, that can be included in the estimate of the conditional probability, $P(X_{t+1}|X_t, \ldots, X_{t-n},)$, is constrained by working memory

Figure 2



Dual algorithm model of sequence learning. **(a)** *Learning transitional probabilities*. Typing the word 'brain' on a keyboard is a temporally organized series of responses. Each letter key (e.g., 'b') is a stimulus, *U*, that corresponds to a particular internal sensorimotor plan represented as a latent state (*X*), that initiates a response, *Y*, at time *t*. With training, learning transition probabilities between events increases the efficiency of sensorimotor processing for subsequent events, leading to increased speed and more accurate selections when the expected event occurs. **(b)** *Building action sets*. Over time, once the transition probabilities between serially ordered items (e.g., 'b', 'r', 'a', 'i', 'n' in 'brain') becomes deterministic, it is computationally efficient to group sensorimotor decisions into unified sets, for example, a 'chunk', where the entire set is represented as a single, generative sensorimotor decision, *W*, and sequences of bound sets of actions can then be the target of learning, that is, $P(W_2|W_1)$.

capacity [34]. One way to overcome this memory limitation is to learn the hierarchical organization of movements and bind sequences of actions into sets or 'chunks' [35]. Returning to the typing example, after extensive practice the plan to execute the set of key presses 'b', 'r', 'a', 'i', and 'n', can be represented internally as a single action decision 'b-r-a-i-n', where actions are coarticulated together in a unified manner (Figure 2b). While each action within the bound set carries its own execution noise, the action initiation decision shifts from waiting for individual sensory cues to automatically triggering one item after another without reliance on sensory cues. Using

an optimal control theory framework, Ramkumar *et al.* demonstrated that as animals become more experienced at a sequential skill, efficiency increases as the number of chunks decreases, reflecting more bound elements in each chunk, while simultaneously minimizing the overall computational cost during learning [36•]. Therefore, binding actions into sets or chunks may represent a critical step in finding the optimal solution to the problem of complex sequential movements, where action sets can themselves be formed at multiple levels of movement hierarchy (e.g., goals, plans, execution).

The orgnanization of serially ordered behaviors into unified sets is often controlled experimentally by making the transition probabilities between cued actions completely deterministic. This can be done by explicitly presenting the sequential order before production [37] or through extensive practice on short action sequences [38]. Behaviorally both approaches lead to slower responses to the first item in the set than to subsequent items in the series [38–43]. This slowing could be due to the fact that the first item in the set has no preceding event with which to estimate the transition probability or the result of the increased time associated with loading the motor buffer [38]. While this first item slowing has classically been used as a behavioral signature for sensorimotor 'chunking', it is not sensitive to detecting whether the responses within the set are bound together under a shared motor decision, nor does it easily allow for looking at the natural evolution of sensorimotor sets during learning.

More recent research has focused on the concept of binding by looking at correlations between temporally adjacent movements within a common set. Several studies in both human and non-human primates show that it takes days of practice or longer to detect the emergence of binding between serial actions under a shared motor command [36,44,45]. For example, Verstynen and colleagues found a dissociation between simple decreases in response time during sequence production, observed during a single session of training, versus correlations in response times between serially ordered actions, that did not emerge until after several days of training [45]. This correlation between temporally adjacent actions is consistent with the binding hypothesis in that it is what would be expected if multiple movements were initiated under a common generative motor command.

The ability to detect binding in sequential responses, as opposed to demarcation of chunk boundaries with the first item slowing, opens the door for asking questions about where in the sensorimotor hierarchy this binding occurs over the course of learning. Recently, Lynch and colleagues adopted a novel remapping paradigm that dissociates learning ordered sets of visual cues, across days of training, from learning ordered sets of finger movements [46•]. Relying on the same correlation measure as Verstynen *et al.* (2012), we found that action binding was stronger when sequences were learned in the sensory domain than when they were learned motorically. Importantly, the level of explicit awareness of the sequence, and thus reliance on declarative processes, was not affected by whether a visual or motor sequence was learned. Of course this does not necessarily exclude the possibility that binding occurs in motor representations [47]. Multivariate pattern analysis approaches have recently opened the door to exploring the nature of action representations with neuroimaging tools like fMRI. Using this approach, Weistler and Diedrichsen showed that cued sequence sets, akin to explicitly cued chunks, can be reliably decoded from population-level activity in higher order motor cortical areas, such as the supplementary motor area (SMA) [48]. Later work by the same group showed that, while the patterns of activity for individual fingers are organized in the primary motor cortex (M1) according to the natural statistics of everyday hand use [49•], the population level activity of M1 itself does not appear to distinguish well-learned sets of actions [50]. Instead, the patterns of task-related activity in upstream premotor regions, such as the dorsal premotor cortex, more reliably distinguished between learned sets of actions [50] (see also [51]).

Mechanistically the implementation of this binding process appears to rely, in part, on basal ganglia (BG) pathways (but see [52]). For example, patients with Parkinson's Disease (PD) have deficits in chunking ability when they are in low dopamine states [53]. At the neural level, cells in the striatum, the main input nucleus to the BG, become tuned to bracketing segments of sequential actions over time, particularly as action sequences become habitual [54,55]. Based on the variety of action sequence-linked cell types in the striatum, Jin and colleagues [56•] proposed that during learning, the striatum facilitates concatenating, or binding actions together. As this binding process unfolds and action sets become established, a subset of cells in the striatum, likely in more executive regions, become sensitive to the initiation of the bound set of actions [56•,57–59]. Since the BG are thought to gate motor responses, this onset sensitivity of striatal cells is consistent with the notion that the entire sequence set becomes a unique action decision that gets triggered by BG pathways.

Conclusion

The emerging behavioral and neuroscientific evidence points to a continuum of interacting algorithms that contribute to the long-term consolidation of sequential skills. Fast associative processes estimate the transition probabilities between serially ordered events so as to improve the speed and efficiency of stimulus-response gating. These associative mechanisms appear to primarily target the processing of sensory signals, but may also

impact downstream motor processes. As the transition probabilities between actions become deterministic, computational complexity is reduced by having reinforcement learning processes unify sets of actions and initiate the bound set as a single decision. Thus the initiation of subsequent actions no longer depends on sensory cues, but on the state of the preceding actions in the set. Signatures of this binding mechanism are associated with motor planning, but can be moderated by upstream sensory processing as well (e.g., [46•]). Rather than reflect serial stages of processing, these associative and binding mechanisms appear to interact during the consolidation process to support balancing goals of making fast and accurate responses while also reducing computational complexity through the establishment of hierarchical structure in motor representations.

The distributed and interacting nature of the associative and binding algorithms makes distinguishing them experimentally challenging; however, the current evidence does provide some clues. For example, binding should only occur when transition probabilities between stimulus-response events are deterministic. Prolonged training on sequences where some of the transitions between items are probabilistic [60], while others are deterministic, should result in no correlations in response times for the non-deterministic transitions. In addition, while binding processes are disrupted in patients with Parkinson's disease [53], we would expect these patients to still have an intact ability to learn transition probabilities. By contrast, patients with damage to the hippocampus should show a combined disruption in both predicting transition probabilities and response binding. These predictions present a roadmap for future research.

Conflict of interest statement

Nothing declared.

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