Trends in
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Review

Online planning of sequential actions

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Natural behavior unfolds as a continuous stream of actions. Because these actions often occur in rapid succession, the brain must prepare multiple future actions while the current action is being executed—a process we refer to as online planning. We review evidence for online planning in unpredictable movement sequences and consider neural implementations that could support parallel execution and multiple planning processes. We then show how this new framework could apply to the learning of specific sequences, improving performance while retaining the ability to modify sequences online. Online planning, therefore, provides a unifying account of how both unpredictable and well-learned sequences are produced, and how training leads to skillful and coordinated performance while retaining behavioral flexibility.

Highlights

New experiments reveal that multiple future actions are planned online during ongoing movement. The overlap of multiple planning processes allows for the generation of fast movement sequences, even if the sequence is not learned.

Future actions are planned, at least to some degree, independently of each other, as one future movement can be replanned without disrupting the initiation of another movement.

Future action plans can influence one another to provide biomechanically efficient transitions between movements.

Online planning may occur in nearly orthogonal neural dimensions to allow for the independence of different processes while permitting the exchange of information.

Online planning is also hypothesized to underlie the production of learned, memory-driven sequences.

Online planning: Coordinating sequences of actions

In many real-world behaviors, individual movements follow each other in rapid succession. To smoothly execute such **action sequences** (see Glossary), the **planning** of future actions must overlap temporally with both the planning of other upcoming actions and the ongoing movement (Figure 1A). The simultaneous control of ongoing movements and the preparation of future actions is referred to here as **online planning**.

In contrast to real-world action sequences, experiments investigating movement planning and execution are typically structured into discrete trials. Each trial starts with the presentation of a stimulus that indicates the **action** to be performed, followed by its execution. A short interval between trials allows the motor system to reset, making each trial independent of the previous one (Figure 1B). Using this controlled approach, a great deal has been learned about the processes that intervene between the identification of a stimulus and the beginning of response execution (here collectively referred to as planning).

This separation of behavior into discrete trials, however, cannot address how processes related to different actions overlap in time. Coordinating such overlap poses a key challenge for the brain, which must prevent the planning of future actions from interfering with ongoing movement [1] while still allowing planning processes for successive actions to interact in ways that support smooth transitions [2–5]. How does the brain achieve this feat? In this review , we address this question first in the context of unpredictable sequences, where we can experimentally control how far individuals can plan ahead. We then build on these insights to consider how online planning shapes the learning of regular, predictable sequences.

Empirical evidence for online planning

What is the evidence that online planning occurs? A first indication comes from human gaze behavior during natural object manipulation. Humans typically fixate on the object relevant to the current action. However, in a sequence, the gaze often shifts to the next task-relevant object even before the current object is reached—likely to gain information to plan the next movement [6–8]. This suggests that the intake of sensory information and planning of the next action overlap

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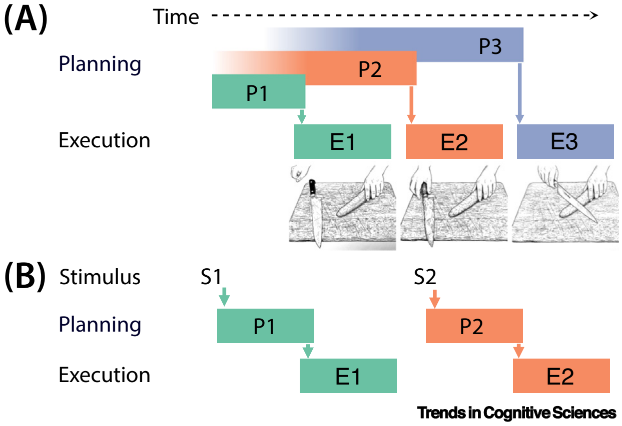

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Figure 1. Online planning. (A) In real-world behavior, different actions, such as grasping a carrot, reaching for a knife, and chopping the carrot, occur in rapid succession. The planning processes of future actions (P2 and P3) must occur in parallel to each other and in parallel to the execution of the current action (E1). (B) Most experiments are structured into discrete trials, such that planning (P) and execution (E) of different actions are separated in time.

with controlling the current action (Figure 1A). Indeed, the idea of pipelining during saccade generation [9] shares many features with the idea of online planning during manual actions discussed here.

A second important piece of evidence comes from studies in which participants produce unpredictable action sequences, with each action prompted by an external cue. By varying the number of cues that can be seen ahead, researchers can infer how many actions into the future are planned. For example, in one finger sequence task [10], where actions were cued by digits on a screen, participants could view only a fixed number of digits ahead (viewing window, Figure 2A). Performance improved with increasing viewing window sizes, demonstrating that participants indeed planned ahead. Eventually, however, showing additional digits did not lead to any further performance improvements, suggesting that the planning horizon was limited to three actions (Figure 2B). Similarly, another study [11] used a continuous control task in which the participants kept a cursor on a moving path (Figure 2C). With an increasing viewing window size, performance improved until it plateaued at about 12 cm (Figure 2D). Both studies, therefore, indicate that participants planned either a finite number of movements or a finite time ahead.

Is the size of the planning horizon fixed, or can it be improved? In both studies, the measured planning horizon increased slightly as participants were trained for multiple days on random sequences. However, the increase was relatively modest. In the finger sequence task, the planning horizon increased from just over three items to just under four. A more important effect of training was that trained participants showed larger performance benefits from the same advanced information. Specifically, the difference between the trained and untrained groups was bigger for large viewing windows (Figure 2B,D). This suggests that while trained participants were able to plan even a single movement faster, the main improvement with training arose from the ability to smoothly coordinate the planning processes of multiple future movements.

The final piece of evidence for online planning is the coarticulation of movements within a sequence. For example, in a sequence of reaching movements, each reach is curved to minimize changes in movement acceleration when transitioning from one target to the next [3,12]. In speech production, syllables are articulated in a way that allows them to blend more smoothly into the next syllable [13]. When spelling letters using American Sign Language, hand gestures

Glossary

Action: the elementary unit of a sequence, such as a reach, a finger press, an eye movement, a hand gesture, or a spoken syllable. While individual actions can be viewed as a temporally evolving sequence of muscle commands, we hypothesize that these are controlled as a single unit at a lower level of the motor hierarchy.

Action sequences: multiple actions that follow rapidly one after another. Movement or action sequences can be stimulus-driven or learned.

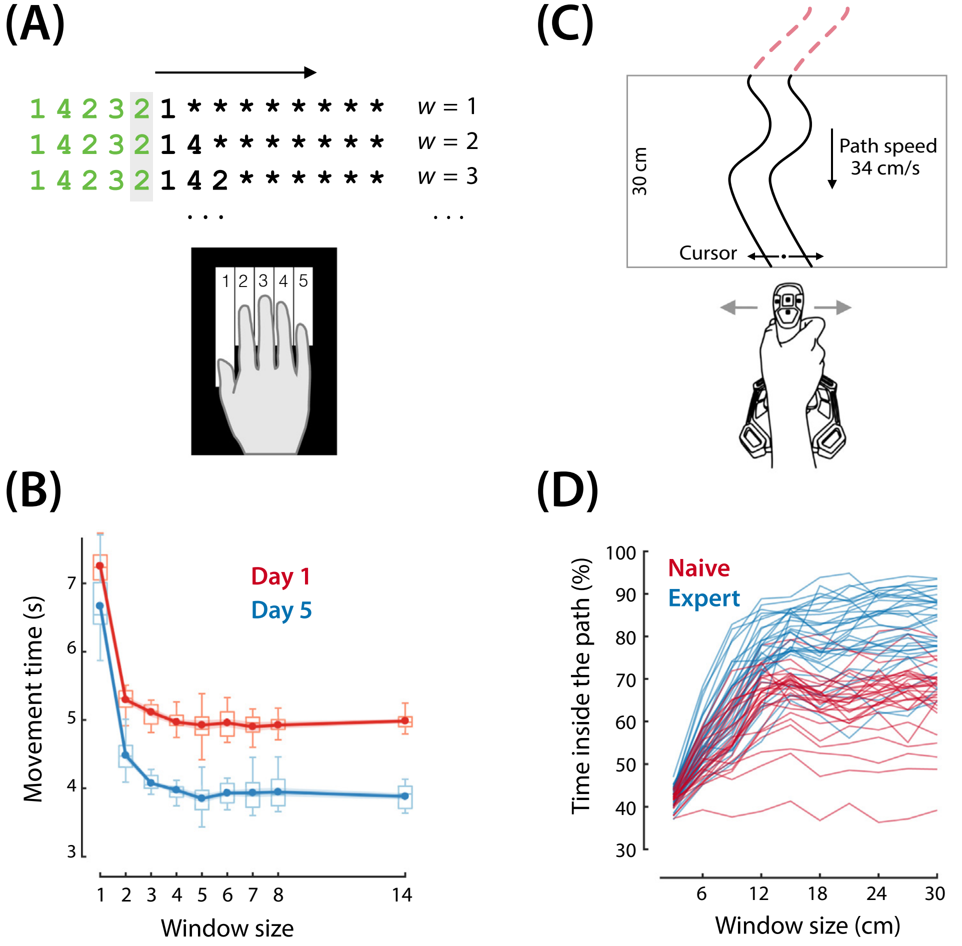
Chunk: a short subsequence of actions that is memorized and controlled as a single unit.

Online planning: planning processes that occur during the production of a sequence.

Planning: here, a broad term that includes all processes between stimulus identification and the onset of action, including the identification of the imperative stimulus (or memory retrieval), the selection of an action, and the preparation of the motoric details of the movement. In other papers, the term '(motor) planning' may only refer to the processes that ready the motor system to produce the action.

Pre-planning: planning processes that occur before the start of a sequence.

Sequence-specific learning: the observation that training on a specific sequence improves the performance of that sequence compared to when the same elementary actions are executed in a different order.



Trends in Cognitive Sciences

Figure 2. Estimating the planning horizon using viewing window experiments. (A) In a finger-sequencing task [10], participants were instructed to produce a fast sequence of finger presses, as instructed by numbers displayed on a screen. Completed finger presses are shown in green. Participants saw a variable number of digits ahead of the last completed press (gray box). Viewing window sizes (W) from 1 to 3 are shown. With each press, a new digit was revealed. (B) Movement time for unpredictable 14-digit sequences decreased with increasing viewing window sizes up to three to four items, suggesting that participants only planned a limited number of items ahead. While participants became faster after training on unpredictable sequences (blue, day 5), the viewing window size only increased slightly. (C) In a driving-like task, a cursor needed to be kept on a continuously moving path by moving a joystick [11]. The path was shown to the participants using viewing windows of varying sizes. (D) Time spent on path increased as a function of viewing window size up to ~12 cm but plateaued afterward. After training on unpredictable tracks (blue, experts), accuracy increased, but the viewing window only increased slightly.

are adjusted depending on the upcoming letter [5]. For such changes to occur, future movements need to be planned to the extent that they can influence how the current movement is executed.

What exactly is planning?

We use the term ‘planning’ for the entire cascade of processes that unfold between the presentation of the imperative cue and the onset of the movement. This includes the identification of the stimulus, the selection of the next action based on that stimulus, and the preparation of the motor system to produce the selected movement accurately. Improvements in the speed of sequence production could arise from any of these processes being performed in parallel with ongoing execution. So, which of these processes occur during online planning?

The fact that movements are coarticulated to biomechanically optimize sequence transitions—even when they have to be planned on the fly [14]—clearly suggests that at least the next two future actions are planned to a motoric level before their execution begins. This is because optimizing the current movement requires knowing how the upcoming movement will be performed.

On the other hand, speed benefits from online planning (Figure 2) could arise at any stage that requires processing time. How long each stage takes will strongly depend on the exact paradigm. Action selection, for example, can be either slow or fast, depending on the complexity of the mapping between stimuli and responses (S-R mapping). When actions are cued with symbols or numbers (e.g., using the numbers 1–5 to indicate the fingers from thumb to pinkie [15]), reaction times often exceed 400 ms [10,16,17]. In contrast, when reaching movements are cued by the presentation of spatial targets directly in the workspace of the subject, actions can be initiated within 200 ms [12,17–19]. This suggests that the mapping between spatial targets and reaching movements is direct and does not require a time-consuming S-R mapping process [20–22]. The fact that the effective planning horizon (the window size that yields behavioral benefits) appears to be somewhat shorter for sequences of spatially cued reaching movements than for numerically cued finger movements suggests that some part of online planning is indeed concerned with action selection. This idea is supported by a recent paper on the **pre-planning** of action sequences [23]. While the reaction times to initiate sequences usually increase with the number of sequence elements [10,24], this review [23] showed that such reaction time costs can be absent when reaching movements are spatially cued.

As with action selection, the complexity of 'motor planning'—that is, the specification of the exact movement parameters once the action is selected [25,26]—can vary widely across paradigms. For spatially cued reaching, it has been argued that the motor system can be brought into the correct initial state almost instantaneously [19]. On the other hand, the initiation of a complex multi-finger hand movement (chord) takes ~270 ms longer than the initiation of a single finger movement, even when the cues and the number of action choices are matched across these two situations [27]. The fact that online planning shows a larger benefit for sequences of chords than for sequences of single finger movements suggests that movement parameters can at least be partly specified during online planning. The same study, however, also compared the neural activity when two planning processes overlapped to when they could be performed sequentially. The extra activity for overlapping (online) planning occurred in posterior parietal regions and was independent of the motoric complexity of the actions [27], suggesting that this extra neuronal activity was associated with parallel processes of response selection rather than movement planning.

In summary, online planning is likely concerned with both 'cognitive' action selection and 'motoric' action planning, with the former being more costly in terms of processing time and neural activity. However, it has also become increasingly clear that action selection and motor planning are tightly interlocking and temporally overlapping processes [28]. For example, the dorsal premotor cortex represents the movement direction of multiple action choices simultaneously, even before a decision is made [29,30]. Thus, it may be difficult to always cleanly separate 'cognitive' and 'motoric' processes, and both may be important for the development of sequential motor skills.

Pre-planning versus online planning

Here, we focus on online planning as a new window onto sequential movements; however, the idea that sequences are pre-planned before movement onset has a long history [14,24]. Behavioral studies have shown that movement sequences that can be pre-planned are executed more quickly [16,31]. At the neural level, at least the first two movement elements of a sequence can be decoded from premovement activity in prefrontal and parietal areas [32,33] and can be elicited with stimulation [34]. Such findings have lent support to the competitive queuing hypothesis [35], according to which all movement elements of a short sequence are prepared in parallel before the first movement starts, with a gradient of activation from the first to the last movement ensuring that the elements are executed in the correct order. Thus, for sequence pre-planning, there is good evidence that multiple future movements can be planned independently and in parallel. This characteristic appears to generalize to online planning. This raises a critical question: to what degree does online planning rely on the same processes as pre-planning, with the only difference being that pre-planning occurs before and online planning occurs during the sequence?

Several lines of evidence suggest that sequence pre-planning and online planning are indeed tightly related. For instance, the capacity for pre-planning and online planning is quite similar. In finger sequences, participants plan approximately three movements ahead online [10]. Similarly, when participants are allowed to pre-plan long sequences of movements, they are faster at executing the first three presses of that sequence, but then slow down to the same speed as when they are not able to prepare the sequence [16].

A recent fMRI study in humans [36] directly compared the neural processes underlying pre-planning and online planning by contrasting complex with simple sequences. Before movement onset, complex sequences engaged premotor and parietal areas more than simple sequences, likely due to the increased demand on pre-planning. The same areas were also more activated during the execution of complex sequences, reflecting the greater demand on online planning. The two patterns matched remarkably well, suggesting that pre-planning and online planning recruit the same premotor–parietal network.

Other evidence, however, suggests that there may be differences between movement pre-planning and online planning. When deciding between two possible reaching movements, participants bias their decision based on biomechanical factors. This bias is smaller when movements are planned online than when they can be pre-planned [2]. Differences could also be observed in the aforementioned fMRI study—while the neural activity patterns for pre-planning and online planning was highly correlated, the match was not perfect [36], suggesting that there are some subtle differences between the two processes.

Independent versus interdependent online planning

If multiple future actions are planned in parallel, are they planned independently, or do their planning processes interact with one another (Figure 3A)? The simple fact that movements are often coarticulated suggests that planning the action two steps ahead (P2) can influence the planning of the next action (P1). Such codependence could arise in two ways. One possibility is that there is unintended crosstalk between the two action plans, biasing the +1 action to become more similar to the +2 action. In general, however, this does not often seem to be the case. For example, in reaching, if the second target is directed to the right, the first reach will be curved to the left [37,39]. In hand spelling, signers often emphasize the differences between subsequent letters to make the transition between them clearer [5]. These findings indicate that the motor system actively optimizes the transition between movements, rather than simply mixing future movement plans [18,37].

In the extreme, multiple actions could be planned and controlled as an inseparable unit (Box 1), such that it is not possible to change one without replanning the other. This prediction was tested directly using perturbation in a finger-sequence task [38] and a spatial reaching task [39] where the cue for the +2 action (Figure 3C,D) was changed during the execution of the current action (+0). Consistent results emerged from both paradigms: while the perturbation delayed the +2 action—indicating that participants indeed had to replan that action [52]—the +1 action was

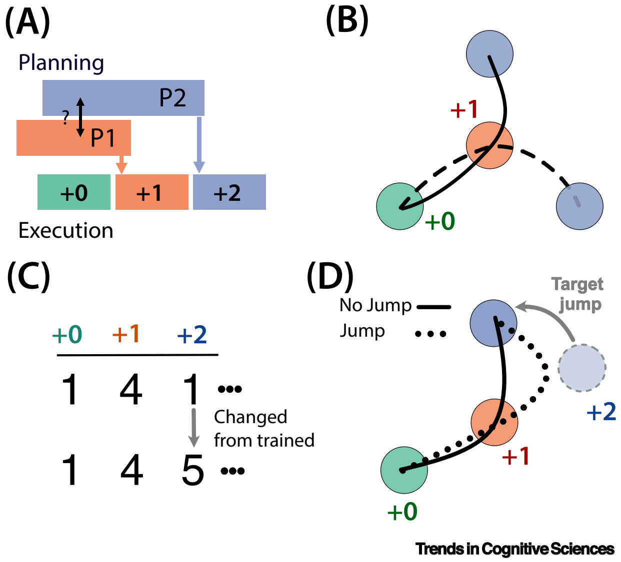


Figure 3. Independent and interdependent planning of future actions. (A) During the execution of the current (+0) action, the planning processes for the next two future actions (+1 and +2) overlap. How do these two processes interact? (B) The reach to the +1 target is curved to make the transition to the +2 target easier. This means that the action planning P2 influenced P1, possibly due to the fact that the two actions are planned together as a unit [37]. (C) Perturbation experiments, however, suggest that the action plans remain at least partly independent. In the finger-sequence task [38], the digit for the action two steps ahead (+2) is changed from a trained sequence when the participants pressed the current key (+0). The execution of the +1 action is not delayed while the +2 action is being replanned. (C) In the arm-reaching task [39], the target for the reach two steps ahead (+2) jumped to a new location, as participants completed the reach to the current target (+0). Again, the +2 reach was replanned without disrupting the execution of the +1 reach.

not delayed. If the +1 and +2 actions had been planned together as a single unit, the +1 action should have been affected as well. These findings show that the two action plans were independent, in the sense that one could still be used to control the next action while the other was replanned.

Taken together, these results indicate that different planning processes for future actions can interact with one another without individual plans losing their ability to be changed when necessary.

Box 1. Continuous versus chunked planning

In this review, we summarize evidence that future movements are not planned independently, but that their planning processes can influence each other. Such codependence could occur in two ways. First, movements could be continuously planned with a fixed horizon into the future [11], and different movement plans could interact within this planning window. As one movement is completed, movement plans are continuously updated such that the sequence can be executed without interruption. In this scenario, the planning horizon could span a specific number of actions, or it could slowly diminish into the future, such that actions further into the future influence the current movement less than those that follow immediately. In control theory, this type of mechanism is called receding horizon planning [40] and provides a powerful—yet computationally efficient—way to optimize sequences of movements.

Alternatively, the planning of future movements could occur in a discrete or chunked fashion—with a group of movements being planned together, then executed, after which the next chunk of movements is planned [41,42]. Because the planning of a new chunk takes time, there should be longer time gaps between chunks than between movements within a chunk [43,44]—indeed, this is the measure by which chunking is commonly defined. It has been suggested that chunking is a mechanism to save cognitive resources for planning [18]. Furthermore, chunks may be the basic unit of motor memory—it has been shown that if learned chunks reoccur in the context of a new, random sequence, participants perform them faster [43,45].

While there is substantial neural and behavioral evidence for chunking [45,46], many issues remain. The temporal gaps between different movements are often dictated by biomechanical requirements. Once these differences are accounted for, the chunking structure for individual subjects seems to change during learning [47], including the merger of smaller chunks into larger ones, as well as the recombination of elements into new chunks [48,49]. Currently, there is no model of chunking or hierarchical action organization that can support such flexibility without the loss of acquired motor skills. Furthermore, perturbation experiments [39,50] (Figure 3) show that changing a single movement does not necessitate replanning the entire chunk. Finally, the inclusion of small 'snippets' of trained sequences in a new random sequence appears to lead to faster performance, without these snippets necessarily aligning with chunk boundaries [12,51].

Neural architectures for online planning

How are multiple planning processes implemented in the brain, such that they do not interfere with ongoing execution processes? And how can they interact with each other while still retaining partial independence?

Our current understanding of how sequential actions are represented in the brain relies heavily on single-neuron recordings in nonhuman primates. A set of early studies demonstrated that single neurons in the supplementary motor area (SMA) and the dorsolateral prefrontal cortex encode not only the upcoming movement but also the specific order of movements within a sequence [53,54]. For instance, when macaques produced a three-movement sequence of hand actions (e.g., push-turn-pull), specific SMA neurons fired selectively when a particular action occurred in a specific sequence, but not when the same action was executed in a different sequential context.

These findings align with a hierarchical model of sequence representation, where frontal regions represent abstract sequence information independent of kinematics and then transfer that information to other motor cortical areas as required for the execution of each action separately. Such a strict hierarchical organization would easily accommodate parallel planning and execution. However, many electrophysiology studies suggest that both planning- and execution-related activity occur in the same cortical areas [55], and even in the same neurons [56,57]. This mixed selectivity has made it difficult to explain how the brain prepares future actions while simultaneously executing current movements.

The analysis of neural population activity using a state-space approach [58] provides an important insight. In this framework, the firing rate of each neuron represents one dimension in a multidimensional neural state space. The instantaneous activity of the entire population maps onto a specific coordinate, and the change in population activity can be visualized as a trajectory through this space (Figure 4A; see [59] for review). A key feature of the neural activity before and during reaching movements is that planning and execution processes evolve in orthogonal subspaces within this multidimensional neural state space [59,60] (Figure 4B). Downstream neurons, therefore, can be insensitive to activity in the planning subspace, allowing the brain to prepare a movement in the primary motor cortex without triggering premature muscle activity.

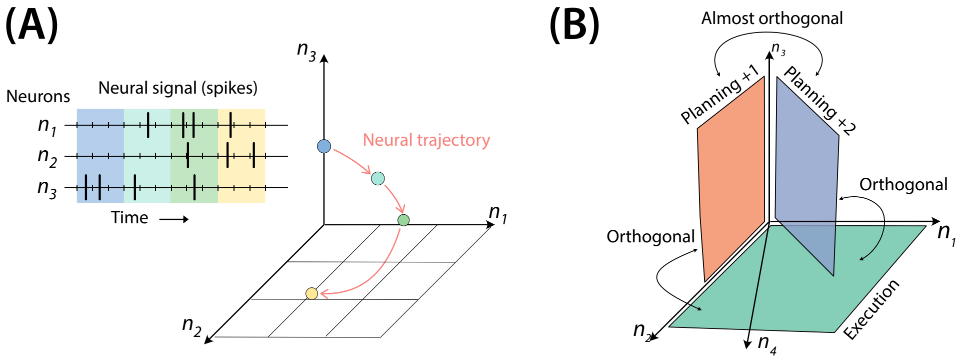


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Figure 4. Neural architecture for online planning. (A) In neuronal state-space analysis, the population activity of n neurons is plotted as a neural trajectory in n-dimensional space (figure adapted from [58]). (B) In this space, planning-related information is encoded in neuronal dimensions that are orthogonal to the neural dimensions that encode execution-related information [1]. We hypothesize that different future movements are encoded in dimensions that are almost, but not fully, orthogonal to each other.

A recent study [1] showed how the motor system also exploits this orthogonality to handle online planning during sequential arm movements. Macaque monkeys were trained to perform two reaches, either as two elements in isolation or in rapid succession as part of a sequence. The same planning and execution subspaces were found to be engaged during isolated movements and during sequence production. Specifically, while the first reach was being executed, there was activity in the primary and premotor cortices along the same neural dimensions as when the second reach was prepared in isolation. This finding suggests that orthogonal subspaces allow the motor system to control the current action while simultaneously preparing the next action in the same brain area without interference [61].

Although such independent subspaces account for the capacity of online planning, they leave open many questions. For example, how are the planning processes for two future actions (movement +1 and +2 in Figure 3) organized? For pre-planning, the competitive cueing hypothesis [32] holds that multiple actions can be planned independently of each other. However, temporally adjacent movements are often coarticulated, which requires that the two planning processes interact with each other. A model with strict independence between planning subspaces cannot explain coarticulation.

One possible architecture is that activity related to future planned actions occurs in separable, but not perfectly orthogonal, subspaces (Figure 4B). The fact that these planning subspaces occupy largely orthogonal dimensions allows for the replanning of one movement without severely disrupting the other [39]. However, the overlap of the two neural dimensions may permit enough interactions to produce a coarticulated movement. In essence, the hypothesized architecture enables the optimization of multiple movements together [18,37] without binding the two into an inseparable unit or **chunk**. Such modular but nonetheless interacting subspaces have been shown to provide a powerful mechanism in perceptual and cognitive tasks [62,63]. Testing this proposed model will require neural data for longer sequences with overlapping movements that demand online planning during execution.

Consequences for sequence-specific learning

If online planning is the main mechanism by which unpredictable sequences are performed, then it has profound consequences for our understanding of how repeated sequences are learned. The ‘classical’ view is that a well-learned sequence may become represented as a single effector-specific motor program, possibly encoded in the primary motor cortex [64,65], with longer sequences broken up into movement chunks (Box 1) that are similarly encoded [46]. Apart from the fact that there is little evidence for the dedicated representation of sequences in the primary motor cortex [1,45,66–69], this idea also has difficulty explaining how the movement-by-movement planning of novel sequences transitions to a qualitatively different control of well-trained sequences.

Online planning offers an alternative perspective. Even well-trained sequences may be planned online, with the only difference being that planning is not triggered by an external stimulus but rather by a memory representation. This idea naturally explains how a stimulus representation and a newly formed memory are combined early in learning [38]. The formation of a sequence-specific memory begins with the first trial—this early trace can already be seen in the second execution of the same sequence, which is faster than the first [70,71]. This improvement occurs not only when the entire sequence is repeated but also when small parts of a sequence (four or more elements) reoccur [51]. This finding suggests that the memory trace supporting this early learning operates on a similar time horizon as online planning.

With further repetitions, learning gains accumulate. For learned sequences, both pre-planning and online planning become faster [16]. This suggests that sequence-specific learning is closely associated with the planning process itself, allowing the system to more quickly recall the required elements and coordinate them within a sequence. The main evidence for this is that the first elements of even untrained sequences, if they can be pre-planned, can be executed as quickly as trained sequences [72]. The main improvements with learning occur for later elements in the sequences that need to be planned online under time pressure [16].

As was the case after a single repetition, the long-lasting sequence memory also seems to consist of small subelements of the sequence. When four to six items of a learned sequence are embedded within a random sequence, they are executed with the same speed as when they occurred within that trained sequence [12]. Importantly, these short, repeated subsequences are executed faster regardless of their position in the original sequence—there is no evidence that they need to align with predefined chunks that the participant has learned (Box 1). Thus, it is possible that the memory traces, such as online planning processes, act continuously.

After extended training, sequences can be produced completely from memory. Neural evidence suggests that the hippocampus is involved in representing this information [73,74]. While memory-driven sequences may be produced by mechanisms completely divorced from the online planning of sequential actions, we think it is unlikely. A recent study [50] shows that even highly learned sequences can be flexibly combined with incoming stimuli. Thus, it is likely that online planning remains the basic control system for sequential action, with the only difference being that long-term memory replaces the imperative stimulus as an input to the system. How exactly motor sequence memories are used in online planning, how they are selected and integrated, is an important question for future research (see Outstanding questions).

The idea that expert performance is supported by motor memories, which are flexibly assembled through a continuous online planning process, may also explain another important feature of motor skills: while some skillful actions are generated so fast that they appear habitual and fixed [75–77], it is a general hallmark of motor skills that experts can flexibly recombine trained elements into new complex sequences [78]. For example, musicians can play the same melody with a different rhythm or emphasis to suit the desired musical expression. Indeed, experiments have shown that the timing and serial order of motor sequences have a modular, flexible representation in premotor and parietal areas [73,79,80], which can then be combined during sequence execution.

Does sequence training always lead to sequence representations that are flexible and modular? A series of studies in rodents suggests that how a sequence is represented may depend on the context in which it is learned. If a rat learns a sequence of three lever presses in isolation, the representation ultimately relies on subcortical areas and is highly automatic. If the same sequence is learned in the context of other sequences, combined with the requirement to switch flexibly between them, it relies on cortical representations [81,82].

For most sequences important for human motor skills, it therefore seems likely that similar control processes are at work for both novice and expert performance, with online planning providing the behavioral flexibility to adjust ongoing sequences to novel goals.

Concluding remarks

Most everyday actions are not produced in isolation, but rather in tight temporal proximity to each other. The resulting action sequences are often malleable and can be adjusted on the fly to fit

Outstanding questions

When and how is information passed from planning to execution processes? After each elementary movement, the execution process needs to be made ready to perform the next movement. Is this information transmission continuous, or does it occur in a phasic fashion?

How are multiple planning processes implemented? Which areas are involved, and how is information updated as the sequence proceeds? Parallel recordings in multiple brain regions and the analysis of their communication should provide novel insight here.

How does online planning relate to working memory? Do the processes related to online planning overlap with those of working memory? Are the capacity limits shared?

How does training on a specific sequence change online planning? What form do sequential memories take? How are they organized so as to avoid interference when learning multiple similar sequences?

Is online planning continuous or chunked? Chunking is often inferred from the temporal organization of sequence production. However, if learned sequences are really controlled in a chunked fashion, the neural state in the controlling areas should change much more at boundaries between chunks than within a chunk.

Do the principles of online planning also apply to language? The production of syllables, words, and sentences has similar computational requirements to sequences of finger and arm movements. Does the brain use similar mechanisms across motor systems, or did the language system develop a specialized scheme?

Does online planning occur for longer time horizons of actions? To organize behavior, goals and subgoals need to be maintained and updated during ongoing behavior over much longer time spans. Do the principles that guide online planning for fast motor sequences also apply to behavior that unfolds over minutes or hours?

current goals and environmental conditions. For example, a basketball player needs to adjust the sequence of running, dribbling, and passing actions based on the movements of other players on the court. The skillful production of such flexible action sequences is an ecologically important and fundamental problem and may be even more important to everyday behavior than the production of fixed action sequences that have received the majority of attention in the literature [83,84]. Thus, a theory of sequential action should start from an understanding of how flexible action sequences are produced, including the process of online planning. We believe that this perspective provides novel insights into the well-studied problems of sequence learning and chunking and offers an avenue for understanding the neuronal underpinnings of sequential actions. It is an open and fascinating question to what degree the principles outlined here also apply to the domain of language production and to the organization of behavior on longer timescales.

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Declaration of interests

The authors declare no competing interests.

References

1. Zimnik, A.J. and Churchland, M.M. (2021) Independent generation of sequence elements by motor cortex. *Nat. Neurosci.* 24, 412–424
2. Michalski, J. *et al.* (2020) Reaching decisions during ongoing movements. *J. Neurophysiol.* 123, 1090–1102
3. Sosnik, R. *et al.* (2004) When practice leads to co-articulation: the evolution of geometrically defined movement primitives. *Exp. Brain Res.* 156, 422–438
4. Krause, P.A. and Kawamoto, A.H. (2020) On the timing and coordination of articulatory movements: historical perspectives and current theoretical challenges. *Lang. Linguist. Compass* 14, e12373
5. Jerde, T.E. *et al.* (2003) Coarticulation in fluent fingerspelling. *J. Neurosci.* 23, 2383–2393
6. Land, M. *et al.* (1999) The roles of vision and eye movements in the control of activities of daily living. *Perception* 28, 1311–1328
7. Land, M.F. and Hayhoe, M. (2001) In what ways do eye movements contribute to everyday activities? *Vis. Res.* 41, 3559–3565
8. Johansson, R.S. *et al.* (2001) Eye-hand coordination in object manipulation. *J. Neurosci.* 21, 6917–6932
9. Jensen, O. *et al.* (2021) An oscillatory pipelining mechanism supporting previewing during visual exploration and reading. *Trends Cogn. Sci.* 25, 1033–1044
10. Ariani, G. *et al.* (2021) The planning horizon for movement sequences. *eNeuro* https://doi.org/10.1523/ENEURO.0085-21.2021
11. Bashford, L. *et al.* (2022) Motor skill learning decreases movement variability and increases planning horizon. *J. Neurophysiol.* 127, 995–1006
12. Kashefi, M. *et al.* (2025) Motor sequence learning involves better prediction of the next action and optimization of movement trajectories. *J. Neurosci.* 45, e0299252025
13. Liu, Q. *et al.* (2018) Anticipatory coarticulation and the minimal planning unit of speech. *J. Exp. Psychol. Hum. Percept. Perform.* 44, 139–153
14. Haggard, P. (1998) Planning of action sequences. *Acta Psychol. (Amst)* 99, 201–215
15. Wiestler, T. and Diedrichsen, J. (2013) Skill learning strengthens cortical representations of motor sequences. *Elife* 2, e00801
16. Ariani, G. and Diedrichsen, J. (2019) Sequence learning is driven by improvements in motor planning. *J. Neurophysiol.* 121, 2088–2100
17. Diedrichsen, J. *et al.* (2001) Moving to directly cued locations abolishes spatial interference during bimanual actions. *Psychol. Sci.* 12, 493–498
18. Ramkumar, P. *et al.* (2016) Chunking as the result of an efficiency computation trade-off. *Nat. Commun.* 7, 12176
19. Haith, A.M. *et al.* (2016) Independence of movement preparation and movement initiation. *J. Neurosci.* 36, 3007–3015
20. Day, B.L. and Lyon, I.N. (2000) Voluntary modification of automatic arm movements evoked by motion of a visual target. *Exp. Brain Res.* 130, 159–168
21. Pruszynski, J.A. *et al.* (2010) Stimulus-locked responses on human arm muscles reveal a rapid neural pathway linking visual input to arm motor output: visual responses on human arm muscles. *Eur. J. Neurosci.* 32, 1049–1057
22. Diedrichsen, J. *et al.* (2004) Independent on-line control of the two hands during bimanual reaching. *Eur. J. Neurosci.* 19, 1643–1652
23. Panjehpour, A. *et al.* (2025) Sequence preparation is not always associated with a reaction time cost. *bioRxiv* https://doi.org/10.1101/2025.11.11.687917
24. Henry, F.M. and Rogers, D.E. (1960) Increased response latency for complicated movements and A "memory drum" theory of neuromotor reaction. *Res. Q. Am. Assoc. Health Phys. Educ. Recreat.* 31, 448–458
25. Wong, A.L. *et al.* (2016) A motor planning stage represents the shape of upcoming movement trajectories. *J. Neurophysiol.* 116, 296–305
26. Wong, A.L. *et al.* (2015) Motor planning. *Neuroscientist* 21, 385–398
27. Shahbazi, M. *et al.* (2024) Neural correlates of online action preparation. *J. Neurosci.* 44, e1880232024
28. Diedrichsen, J. and Kornysheva, K. (2015) Motor skill learning between selection and execution. *Trends Cogn. Sci.* 19, 227–233
29. Cisek, P. and Kalaska, J.F. (2005) Neural correlates of reaching decisions in dorsal premotor cortex: specification of multiple direction choices and final selection of action. *Neuron* 45, 801–814
30. Cisek, P. and Kalaska, J.F. (2010) Neural mechanisms for interacting with a world full of action choices. *Annu. Rev. Neurosci.* 33, 269–298
31. Mantziara, M. *et al.* (2021) Competitive state of movements during planning predicts sequence performance. *J. Neurophysiol.* 125, 1251–1268

32. Kornysheva, K. *et al.* (2019) Neural competitive queuing of ordinal structure underlies skilled sequential action. *Neuron* 101, 1166–1180.e3
33. Gallivan, J.P. *et al.* (2016) Planning ahead: object-directed sequential actions decoded from human frontoparietal and occipitotemporal networks. *Cereb. Cortex* 26, 708–730
34. Behmer, L.P. *et al.* (2023) Motor-evoked potentials for early individual elements of an action sequence during planning reflect parallel activation processes. *Mot. Control.* 27, 498–517
35. Bullock, D. and Grossberg, S. (1988) Neural dynamics of planned arm movements: emergent invariants and speed-accuracy properties during trajectory formation. *Psychol. Rev.* 95, 49–90
36. Ariani, G. *et al.* (2024) Cortical areas for planning sequences before and during movement. *J. Neurosci.* https://doi.org/10.1523/JNEUROSCI.1300-24.2024
37. Kalidindi, H.T. and Crevecoeur, F. (2024) Task-dependent coarticulation of movement sequences. *Elife* 13, RP96854
38. Nazerzadeh, A. *et al.* (2026) Integration of memory and sensory information in skilled sequence production. *J. Neurosci.* 46, e1797252026
39. Kashefi, M. *et al.* (2024) Future movement plans interact in sequential arm movements. *Elife* 13, RP94485
40. Guigon, E. (2023) A computational theory for the production of limb movements. *Psychol. Rev.* 130, 23–51
41. Sternberg, S. *et al.* (1990) Hierarchical control in the execution of action sequences: tests of two invariance properties. In *Attention Performance 13: Motor Representation Control* (53) (Jeannerod, M., ed.), Psychology Press
42. Acuna, D.E. *et al.* (2014) Multifaceted aspects of chunking enable robust algorithms. *J. Neurophysiol.* 112, 1849–1856
43. Sakai, K. *et al.* (2003) Chunking during human visuomotor sequence learning. *Exp. Brain Res.* 152, 229–242
44. Hikosaka, O. *et al.* (2002) Central mechanisms of motor skill learning. *Curr. Opin. Neurobiol.* 12, 217–222
45. Yokoi, A. and Diedrichsen, J. (2019) Neural organization of hierarchical motor sequence representations in the human neocortex. *Neuron* 103, 1178–1190.e7
46. Wymbs, N.F. *et al.* (2012) Differential recruitment of the sensorimotor putamen and frontoparietal cortex during motor chunking in humans. *Neuron* 74, 936–946
47. Popp, N.J. *et al.* (2020) The effect of instruction on motor skill learning. *J. Neurophysiol.* 124, 1449–1457
48. Tosatto, L. *et al.* (2023) The dynamics of chunking in humans (*Homo sapiens*) and guinea baboons (*Papio papio*). *J. Comp. Psychol.* 137, 191–199
49. Tosatto, L. *et al.* (2022) The evolution of chunks in sequence learning. *Cogn. Sci.* 46, e13124
50. Nazerzadeh, A. *et al.* (2025) Integration of memory and sensory information in skilled sequence production. *bioRxiv* https://doi.org/10.1523/JNEUROSCI.1797-25.2026
51. Shahbazi, M. *et al.* (2025) Repetition effects reveal the subsequence representation of actions. *J. Neurophysiol.* 134, 691–697
52. Kalidindi, H.T. and Crevecoeur, F. (2023) Human reaching control in dynamic environments. *Curr. Opin. Neurobiol.* 83, 102810
53. Shima, K. and Tanji, J. (1998) Both supplementary and presupplementary motor areas are crucial for the temporal organization of multiple movements. *J. Neurophysiol.* 80, 3247–3260
54. Tanji, J. and Shima, K. (1994) Role for supplementary motor area cells in planning several movements ahead. *Nature* 371, 413–416
55. Crammond, D.J. and Kalaska, J.F. (2000) Prior information in motor and premotor cortex: activity during the delay period and effect on pre-movement activity. *J. Neurophysiol.* 84, 986–1005
56. Kaufman, M.T. *et al.* (2010) Roles of monkey premotor neuron classes in movement preparation and execution. *J. Neurophysiol.* 104, 799–810
57. Tanji, J. and Evarts, E.V. (1976) Anticipatory activity of motor cortex neurons in relation to direction of an intended movement. *J. Neurophysiol.* 39, 1062–1068
58. Vyas, S. *et al.* (2020) Computation through neural population dynamics. *Annu. Rev. Neurosci.* 43, 249–275
59. Churchland, M.M. and Shenoy, K.V. (2024) Preparatory activity and the expansive null-space. *Nat. Rev. Neurosci.* 25, 213–236
60. Kaufman, M.T. *et al.* (2014) Cortical activity in the null space: permitting preparation without movement. *Nat. Neurosci.* 17, 440–448
61. Bardanikas, G. *et al.* (2026) Reciprocal fronto-parietal interactions support motor anticipation during sequential reaching. *bioRxiv* https://doi.org/10.64898/2026.03.03.709252
62. Ostojic, S. and Fusi, S. (2024) Computational role of structure in neural activity and connectivity. *Trends Cogn. Sci.* 28, 677–690
63. Tye, K.M. *et al.* (2024) Mixed selectivity: cellular computations for complexity. *Neuron* 112, 2289–2303
64. Karni, A. *et al.* (1998) The acquisition of skilled motor performance: fast and slow experience-driven changes in primary motor cortex. *Proc. Natl. Acad. Sci. U. S. A.* 95, 861–868
65. Karni, A. *et al.* (1995) Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature* 377, 155–158
66. Wong, A.L. and Krakauer, J.W. (2019) Why are sequence representations in primary motor cortex so elusive? *Neuron* 103, 956–958
67. Berlot, E. *et al.* (2018) In search of the engram, 2017. *Curr. Opin. Behav. Sci.* 20, 56–60
68. Berlot, E. *et al.* (2020) A critical re-evaluation of fMRI signatures of motor sequence learning. *Elife* 9, e55241
69. Russo, A.A. *et al.* (2018) Motor cortex embeds muscle-like commands in an untangled population response. *Neuron* 97, 953–966.e8
70. Ariani, G. *et al.* (2020) *Repetita iuvant*: repetition facilitates online planning of sequential movements. *J. Neurophysiol.* 123, 1727–1738
71. Johnson, B.P. *et al.* (2023) Generalization of procedural motor sequence learning after a single practice trial. *NPJ Sci. Learn.* 8, 45
72. Wong, A.L. *et al.* (2015) Explicit knowledge enhances motor vigor and performance: motivation versus practice in sequence tasks. *J. Neurophysiol.* 114, 219–232
73. Yewbrey, R. *et al.* (2023) Cortical patterns shift from sequence feature separation during planning to integration during motor execution. *J. Neurosci.* 43, 1742–1756
74. Dolfen, N. *et al.* (2024) The hippocampus represents information about movements in their temporal position in a learned motor sequence. *J. Neurosci.* 44, e0584242024
75. Grundmann, C.C. *et al.* (2025) Studying human habit formation through motor sequence learning. *Cogn. Affect. Behav. Neurosci.* 25, 941–951
76. Du, Y. *et al.* (2022) The relationship between habits and motor skills in humans. *Trends Cogn. Sci.* 26, 371–387
77. Du, Y. and Haith, A.M. (2025) Dissociable habits of response preparation versus response initiation. *Nat. Hum. Behav.* 9, 1941–1958
78. Ranganathan, R. *et al.* (2020) Repetition without repetition: challenges in understanding behavioral flexibility in motor skill. *Front. Psychol.* 11, 2018
79. Kornysheva, K. *et al.* (2013) Interaction of temporal and ordinal representations in movement sequences. *J. Neurophysiol.* 109, 1416–1424
80. Kornysheva, K. and Diedrichsen, J. (2014) Human premotor areas parse sequences into their spatial and temporal features. *Elife* 3, e03043
81. Mizes, K.G.C. *et al.* (2024) The role of motor cortex in motor sequence execution depends on demands for flexibility. *Nat. Neurosci.* 27, 2466–2475
82. Mizes, K.G.C. *et al.* (2023) Dissociating the contributions of sensorimotor striatum to automatic and visually guided motor sequences. *Nat. Neurosci.* 26, 1791–1804
83. Korman, M. *et al.* (2003) Multiple shifts in the representation of a motor sequence during the acquisition of skilled performance. *Proc. Natl. Acad. Sci. U. S. A.* 100, 12492–12497
84. Dayan, E. and Cohen, L.G. (2011) Neuroplasticity subserving motor skill learning. *Neuron* 72, 443–454