Online planning of sequential actions

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Abstract

Natural behaviour unfolds as a continuous stream of actions. Because these typically occur in rapid succession, the brain must prepare multiple future actions while the current movement is ongoing – a process that we call online planning. Here we review the behavioral evidence for online planning and discuss possible neural implementations that would support such parallel preparation and allow for a partial dependence and partial independence between different planning processes. Finally, we argue that training on specific sequences accelerates online planning, thereby 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 and behavioral flexibility.

Highlights

- Multiple future actions are planned during an ongoing movement
- Future actions are planned, at least to some degree, independent of each other
- Plans can influence each other to provide biomechanically efficient transitions between actions
- Improvements in online planning account for a large part of motor sequence learning

Online planning – coordinating sequences of actions

To study behavior, most experiments are structured into discrete trials. Each trial starts with the presentation of a stimulus, followed by some internal processing (here denoted by planning), and finally the response. A short interval between trials ensures that the system can reset, making each trial independent of the previous one (Fig. 1a). This discrete trial structure greatly simplifies the analysis of the behavior of interest.

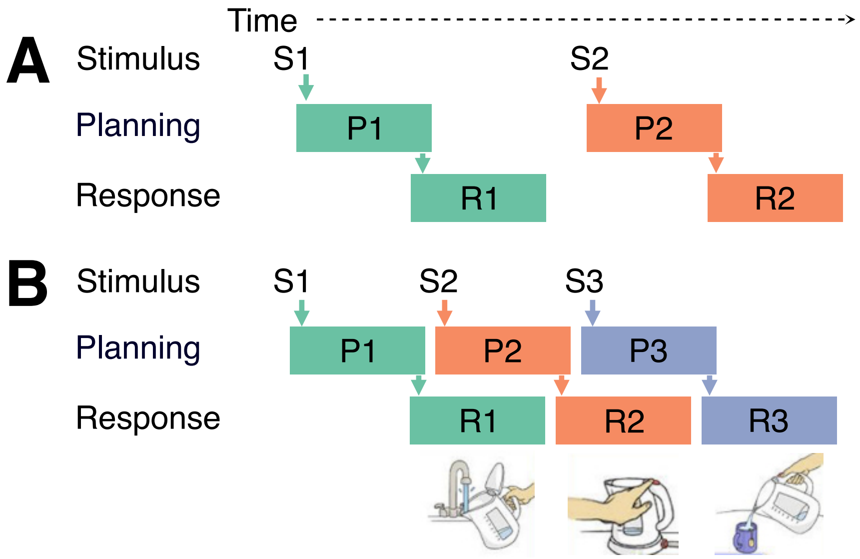

***Figure 1**. Online planning. **(A)** In classical experiments, planning (P) and response (R) phases associated with different actions are separated in time. **(B)** In real-world behavior like making a cup of tea, planning future actions occurs in parallel to the ongoing execution of current actions.*

However, real-world behaviors are much more complex. Movements typically follow each other in rapid succession and may even overlap (Fig. 1b). Moreover, movements are often co-articulated, such that the current movement is shaped to allow for smooth transition to the next movement [1–3].

In this article, we argue that to execute movement sequences smoothly, the nervous system must rely on *online planning*: simultaneously preparing future movements while controlling the ongoing movement. Planning and executing at the same time requires a delicate coordination between different neural processes. On one hand, the planning of future actions must occur independently from the execution-related processes, so that it does not interfere with the ongoing movement. On the other hand, the different processes need to interact, for example, when the current movement is co-articulated to enable a smoother transition to the next [4].

Empirical evidence for online planning

What is the evidence that online planning occurs? One 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 [5–7]. This suggests that the intake of sensory information and planning of the next action overlaps with controlling the current action (Fig. 1b).

A second important piece of evidence comes from studies in which participants produce random movement sequences, with each movement element indicated by an external cue. By varying the number of cues that can be seen ahead, one can infer how many movements into the future participants plan. For example, Ariani et al. [8] used a finger sequence task, cued by digits on a screen. Participants could view only a fixed number of digits ahead into the future (viewing window, Fig. 1a). Performance increased with increasing viewing window sizes, demonstrating that participants indeed planned ahead. However, showing additional digits did not lead to any further performance improvements, suggesting that the planning horizon was limited to three movements (Fig. 1b). Similarly, Bashford et al. [9] used a continuous control task in which the participants kept a cursor on a moving path (Fig. 1c). With increasing viewing window size the performance increased, until it plateaued at about 12cm (Fig. 1d). Both studies therefore indicate that participants planned either a finite number of movements or a finite time ahead.

Is this size of the planning horizon fixed, or can it be improved? In both studies, two changes occurred after multiple days of training on random sequences or tracks: First, the planning horizon increased slightly as participants were able to use information further ahead. More importantly, the trained participants showed larger performance benefits from the same advance information – the difference between the two groups was larger for large as compared to small viewing windows (Figs. 1b and 1d). This shows that, while trained participants were able to plan 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 co-articulation of movements within a sequence. For example, in a sequence of reaching movements, each reach is curved to minimize changes in movement acceleration when going from one to the next target [1,10]. In speech production, syllables are articulated such that they blend more smoothly into the next [11]. When spelling letters using the American sign language, hand gestures are changed depending on the letter that comes after [3]. For such changes to occur, future movements need to be planned to the degree that they can influence how the current movement is executed.

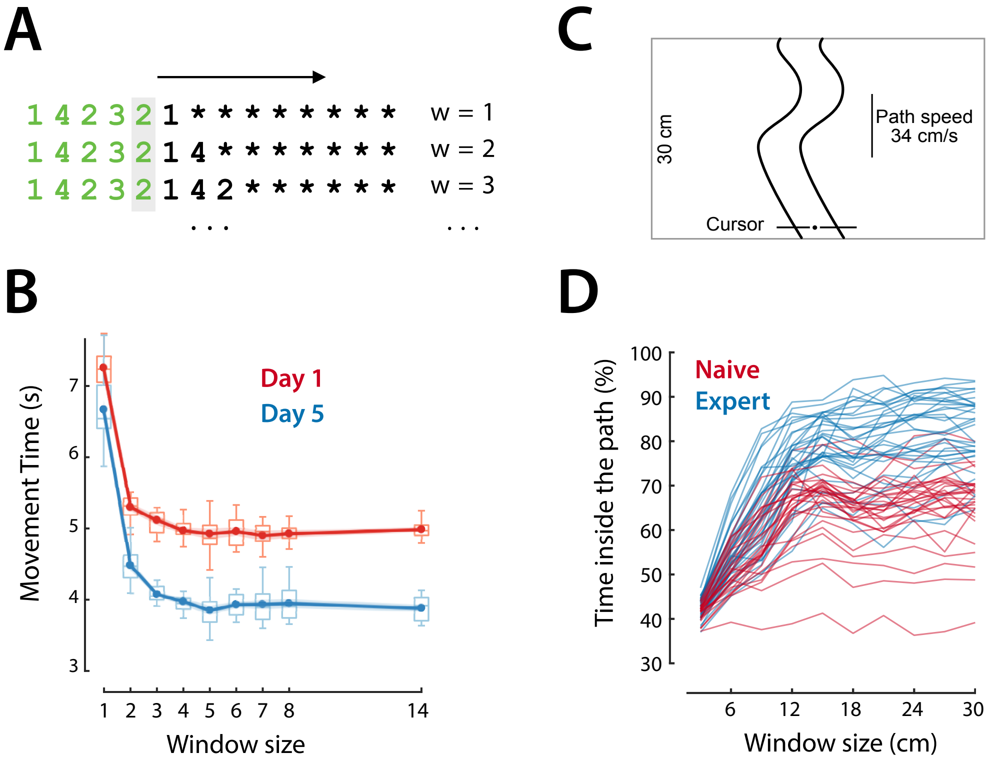

Figure 2. *Estimating the planning horizon using viewing window experiments. (**A**) In a finger-sequencing task* [8], *participants could see a variable number of digits ahead of the current press (gray box). Viewing window sizes (w) from 1-3 are shown. With each press, a new digit was revealed. (**B**) Movement time for random 14-digit sequences decreased as a function of viewing window size and as a function of training (day1 vs. day 5). (**C**) In a car-driving task, a cursor needed to be kept on a continuously moving path* [9]. *The path was shown to the participants using a viewing window of different size. (**D**) Time spent on path increased as function of viewing window size and as function of training (expert vs. naïve).*

What exactly is planning?

In this paper, 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 sensory processes that lead to 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. Which of these processing stages are performed during online planning?

The fact that movements are co-articulated to biomechanically optimize sequence transitions [12] clearly argues that at least the next two future actions are planned to a motoric level before their execution begins, as it is important to know how to do the next movement if one is to optimize the current one. On the other hand, speed benefits from online planning (Fig. 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 [13]), reaction times often exceed 400ms [8,14,15]. 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 200ms [10,15–17]. This suggest that the mapping between spatial targets and reaching movements is very direct and does not require a time-consuming S-R mapping process [18–20]. The fact that the effective planning horizon (the window size for each participants still show 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 [22]. While the reaction time to initiate sequences usually increase with the number of sequence elements [8,21], this paper showed that such reaction time cost is absent when reaching movements are spatially cued.

As for action selection, the complexity of “motor planning”, the specification of the exact movement parameters once the action is selected [23,24], can vary widely across paradigms. For spatially-cued reaching movement it has been argued that the motor system can be brought into the correct initial state almost instantaneously [17]. On the other hand, the initiation of a complex multi-finger hand movements (chords) takes ~270ms longer than the initiation of a single finger press, even when the cues and the number of action choices are matched across these two situations [25]. The fact the online planning benefits for chords is larger than for single finger movements suggest that online planning at least partly can help specify the exact movement parameters. 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 [25], suggesting that this extra neuronal activity was associated with parallel processes of response selection rather than of movement planning.

In summary, it is likely that online planning is concerned both with “cognitive” action selection and “motoric” action planning, with the former likely being the 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 [26]. For example, dorsal premotor cortex represents the movement direction of multiple action choices simultaneously, even before a decision is made [27,28]. 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- vs. online planning

Although we focus here on online planning as a new window onto sequential movements, the idea that sequences are pre-planned before movement onset has a long history [12,21]. Behaviorally, it can be shown that movement sequences that can be pre-planned are executed more quickly [14,29]. Neurally, at least the first two movement elements of a sequence can be decoded from the pre-movement activity in prefrontal and parietal areas [30,31], and can be elicited with stimulation [32]. Such findings have lend support to the competitive queuing hypothesis [33], 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, it is relatively well established that multiple future movement can be planned in parallel. If this is the case, then the critical question becomes to what degree online planning relies on the same processes as preplanning, with the only difference that these would now occur during movement execution, and not before initiation.

Several lines of evidence seem to suggest that sequence pre- and online-planning are indeed tightly related. For instance, the capacity of pre- and online planning appears to be very similar. In finger-sequences, participants online plan approximately 3 movements ahead [8]. Similarly, when participants are allowed to pre-plan long sequences of movements, they are faster in executing the first 3 presses of that sequence, but then slow down to the same speed as when they were not able to prepare the sequence [15].

A recent fMRI study in humans [34] directly compared the neural processes underlying pre- and online planning by contrasting complex with simple sequences. Before movement start, complex sequences engaged premotor and parietal areas more than simple sequences, likely related to the increased demand on pre-planning. The same areas were also more activated during the execution of complex sequences, likely reflecting the larger demand on online-planning. The two difference patterns matched remarkably well, arguing that the same set of areas were involved in both processes.

Other evidence, however, suggests that there may be differences between movement pre- 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 [4]. Difference could also be observed in the beforementioned fMRI study - while the neural activity for pre- and online-planning was highly correlated, the match was not perfect [34], suggesting that there are some subtle differences between the two processes.

Independent vs. interdependent online planning

If multiple future actions are planned in parallel, are they planned independently, or do their planning processes depend on one another (Fig. 3a)? In the extreme, multiple movements could be planned as an inseparable unit (see text box chunked vs. continuous planning), such that it is not possible to change one without re-planning the other. This prediction was tested directly using perturbation in a finger-sequence tasks [35] and a spatial reaching task [36] where the cue for the action two ahead (+2, Fig. 3b,c) was changed during execution of the current action (+0). Consistent results emerged from both paradigms: while the perturbation delayed reaction to the +2 action -indicating that participants had to replan that action- the +1 action was not delayed. If the +1 and +2 action had been planned together as a unit, the +1 action should have been affected as well. These findings clearly show that the two movement plans were at least partially independent.

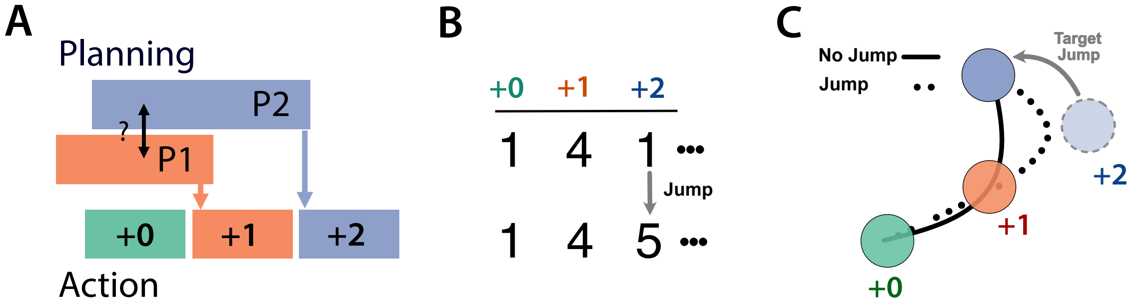

Figure 3. *Independent vs. interdependent planning of future actions.* ***(A)*** *During the execution of the current (+0) action, the planning processes for the next two future actions (+1, +2) overlap. How do they interact?* ***(B)*** *Probing future planning processes using perturbations in the finger-sequence task* [35]. *When the participants press the current key (+0) the digit for the action two ahead (+2) is changed (dashed arrow).* ***(C)*** *Arm-reaching task* [36]. *When the participants reach the current target (+0) the spatial for the reach two ahead (+2) jumps to a new location.*

Future movements plans, however, also must have the ability to interact with each other. The simple fact that movements are often co-articulated suggests the planning of the +2 movement influences the planning of the +1 movement (Fig. 3a). Such co-dependence could be arising in two ways. One possibility is that there is unintended crosstalk between the two movement plans, biasing the +1 movement to become more similar to the +2 movement. 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 movement will be curved to the left. In hand spelling, signers often emphasize the differences between subsequent letters to make the transition between them clearer [3]. These findings indicate that the motor system actively optimizes the transition between movements, rather than simply mixing future movement plans [16,37]. Either way, however, it is very clear that there is a partial dependence between the planning processes of future movements.

Neural architectures for online planning

How are multiple planning processes implemented in neuronal population, such that they do not infer 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 non-human primates. A set of early studies, by Tanji and colleagues, demonstrated that single neurons in the supplementary motor areas (SMA) and the dorsolateral prefrontal cortex (dlPFC) encode not only the upcoming movement but also the specific order of movements within a sequence [38,39]. 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 fit 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 occurs in the same cortical areas [40], and even in the same neurons [41,42]. This mixed selectivity has made it hard to explain how the brain prepares future actions while simultaneously executing current movements.

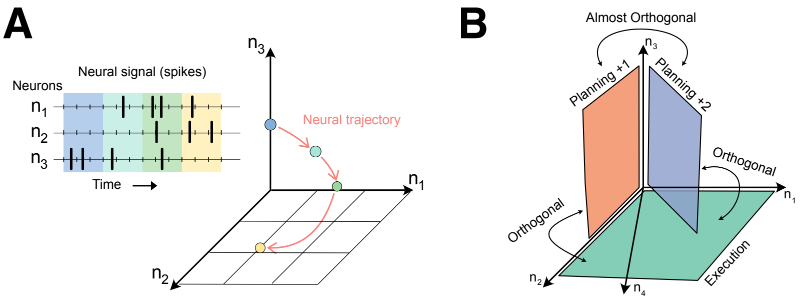

Figure 4. *Neural architecture for online planning.* ***(A)*** *In neuronal state-space analysis, the population activity of n neurons is plotted as a neural trajectory in n-dimensional space.* ***(B)*** *In this space, planning-related information is encoded in neuronal dimensions that are orthogonal to the neural dimensions that encode execution-related information* [43]. *We hypothesize that different future movements are encoded in dimensions that a almost, but not fully, orthogonal from each other.*

The analysis of neural population activity using a state-space approach [44] 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 to a specific coordinate that evolves dynamically through this space (Fig. 4a, see [45] for review). A key feature of the neural activity before and during reaching movements is that planning and execution processes evolve in orthogonal subspaces in this multi-dimensional neural state space [45,46] (Fig. 4b). Downstream neurons, therefore, can be insensitive to activity in the planning subspace, allowing the brain to prepare a movement in primary motor cortex without triggering premature muscle activity.

Zimnik and Churchland [43] recently showed how the motor system also exploits this orthogonality to handle online planning during sequential arm movements. By training NHPs to perform two reaches, either as two elements in isolation or in rapid succession as part of a sequence, they found that the same planning and execution subspaces were engaged during isolated movements and during sequence production. Specifically, while the first reach was being executed, there was activity in primary and premotor cortices along the same neural dimensions as when the second movement was prepared in isolation. This finding suggests that orthogonal subspaces allow the motor system to control the current movement, while simultaneously preparing the next movement in the same brain area without interference.

Although such independent subspaces account for the capacity of online planning, it leaves open many questions. For example, how are the planning processes for two future movements (movement +1 and +2 in Fig. 3) organized? When two planning processes occur together, the two movements are often co-articulated, which requires that the two planning processes to interact with each other. A model with strict independence between planning subspaces cannot explain this.

Here we suggest that activity related to the future planned movements may occur in separable, but not perfectly orthogonal, subspaces (Fig. 4b). We suggest that these planning subspaces are close to orthogonal to allow for replanning of one movement without disrupting the other (as shown in the target-change experiments). However, the overlap of the two neural dimensions may allow enough interactions to produce a coarticulated movement. Such modular but nonetheless interacting subspaces have been shown to provide a powerful mechanisms in perceptual and cognitive tasks [47,48]. Testing this proposed model requires neural data for longer sequences with overlapping movements that demand online planning during execution.

Consequences for sequence 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 primary motor cortex [49,50], with longer sequences being broken up into movement chunks (see text box) that are similarly encoded [51]. Apart from the fact that there is very little evidence for the dedicated representation of sequences in primary motor cortex [52–57], 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 a fresh perspective here: The training of specific sequences does not replace online planning as the main mechanism for sequence generation, but rather it makes online planning faster. The formation of a sequence memory begins with the first trial - this early trace can be seen already in the second execution of the same sequence, which is faster than the first [58,59]. This improvement does not only occur when the entire sequence is repeated, but also when small parts of a sequence (4 or more elements) reoccur [60]. This finding suggests that the memory trace supporting repetition effects operates on very similar time horizon as online planning.

With further repetitions, learning gains accumulate. For learned sequences both pre-and online planning becomes faster [15]. This suggest that the memory 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 for trained sequences [61]. The main improvements with learning occur for later elements in the sequences that need to be planned online under time pressure [15].

As was the case after a single repetition, the longer lasting sequence memory also seems to consist of small sub-elements of the sequence. When 4-6 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 [10]. 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 pre-defined chunks that the participant has learned (see text box, chunked vs. continuous planning). Thus, it is possible that the memory traces, like online planning process, act in a continuous manner.

Overall, we think therefore that it is unlikely that the motor system completely transitions from a continuous online planning process for novel sequences to a discrete memory representation for learned sequence or chunks. Rather, we hypothesize that the control system that uses online planning basically remains the same – and that the newly formed memory trace acts upon this process, accelerating the planning and hence the performance of trained sequence [35]. 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 being flexibly assembled trough a continuous online planning process also explains another important feature of motor skills: while some skillful actions are generated so fast that they appear habitual and fixed [62–64], it is general hallmark of motor skill that experts can flexibly recombine trained elements into new complex actions [65]. 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 has a modular, flexible representation in pre-motor and parietal areas [66–68], that then can be combined during sequence execution.

Does sequence training always lead to sequence representations that are flexible and modular? A series of studies in rats suggest that the neural representation of a sequence may differ depending on the context that it is learned in. If a rat learned a sequence of 3 level presses in isolation, the representation relied ultimately on subcortical areas and was highly automatic. If the same sequence was learned in the context of other sequences, combined with the requirement to switch flexibly between them, it relied on cortical representations [69,70].

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

Concluding remarks

Most everyday actions are not produced in isolation, but rather in tight temporal proximity with each other. The resulting action sequences are often malleable and can be adjusted on the fly to fit the current goals and environmental conditions. For example, a basketball player leading the ball down the field needs to adjust their running, dribbling, and passing actions based on the movements of other players on the field. We argue that the skillful production of such flexible action sequences is an ecologically important and fundamental problem, likely more important than the production of fixed action sequences that has received the majority of attention in the literature [71,72]. 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 provides 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.

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 neurally?** Which areas are involved and how is information updated as the sequence proceeds? Parallel recordings in multiple neural regions, and the analysis of communication between different neural subspaces should provide novel insight here.
- **How does training on a specific sequence change online planning?** What form do sequential memories take? How are they organized as to avoid interference when learning multiple similar sequences?
- **Is online planning continuous or chunked?** Chunking is often inferred from the temporal organisation 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 on 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 as sequences of finger and arm movements. Is the human brain using the similar mechanism across motor systems, or did the language system develop a specialized mechanism?
- **Does online planning occur for longer time horizons of actions**? To organize behaviour, goals and subgoals need to be maintained and updated during ongoing behavior over much longer time spans. Do the principles that guide the online planning for the fast motor sequences also apply to behavior that unfolds over minutes or hours?

Text Box: Continuous vs. chunked planning

In this paper we summarize evidence that future movements are not planned independently, but that their planning processes partly influence each other. Such co-dependence could occur in two ways. First, movements could be continuously planned with fixed horizon into the future [9], 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 [73], and provides a powerful - yet computational efficient - way to optimize sequences of movements.

Alternatively, planning of future movements could occur in discrete or chunked fashion – with a group of movements being planned together, then executed, after which the next chunk of movements in planned [74,75]. Because the planning of a new chunk takes time, there should be longer time-gaps between chunks than between movements within a chunk [76,77] – 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 [16]. Furthermore, chunks may be the basic unit of motor memory – it has been shown if learned chunks re-occur in the context of a new, random sequence, participants perform these faster [53,76].

While there is substantial neural and behavioral evidence for chunking [51,53], a lot of issues remain. The temporal gaps between different movements are often dictated by biomechanical requirements. Once accounting for these difference, the chunking structure for individual subjects seems to change during learning [78], including the merger of smaller into larger chunks, but also the recombination of elements into new chunks [79,80]. Currently, there is no model of chunking or hierarchical action organisation that would be able to support such flexibility without the loss of the acquired motor skill. Furthermore, perturbation experiments [35,36](Fig. 3) show that changing one single movement does not lead to the entire chunk having to be replanned. Finally, the inclusion of small "snippets" of trained sequence in a new random sequence appears to lead to faster performance, without these snippets necessarily having to align with chunk boundaries [10,60] .

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