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Current Opinion in
Neurobiology

From a single decision to a multi-step algorithm

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Humans can perform sequential and recursive computations, as when calculating 23×74 . However, this comes at a cost: flexible computations are slow and effortful. We argue that this competence involves serial chains of successive decisions, each based on the accumulation of evidence up to a threshold and forwarding the result to the subsequent step. Such serial 'programs' require a specific neurobiological architecture, approximating the operation of a slow serial Turing machine. We review recent progress in understanding how the brain implements such multi-step decisions and briefly examine how they might be realized in models of primate cortex.

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Current Opinion in Neurobiology 2012, 22:1–9

This review comes from a themed issue on
Decision making
Edited by Kenji Doya and Michael Shadlen

0959-4388/\$ – see front matter

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<http://dx.doi.org/10.1016/j.conb.2012.05.006>

Introduction: Turing's hunches and rational machines

The mathematician Alan Turing made at least two seminal contributions to computing. First, to help break the German Enigma code, Turing designed a sequential decision algorithm that consists in accumulating votes for the different options and using a threshold criterion to commit to a choice. This framework has become ubiquitous in the psychology and neuroscience of decision making [1,2]. Second, Turing formalized a sequential computing device, the famous 'Turing machine'. Although Turing conceived it as an abstract model of "a man in the process of computing" [3], this idea met with a strong resistance in the neuroscience community and, to this day, is still considered the wrong metaphor for brain-like computing. Part of this resistance is justified: unlike Turing devices, the brain is largely parallel, plastic,

and computes over probability distributions rather than discrete symbols [2]. However, as we review here, conscious rational thought and more generally the assembly of multiple decisions into sequential routines might still be approximated by a Turing machine. We argue that the Turing view of serial computations provides a fruitful first-order approximation of the role of a central executive system in serial decision making and conscious thought.

From isolated decisions to mental programs: the brain's Turing machine

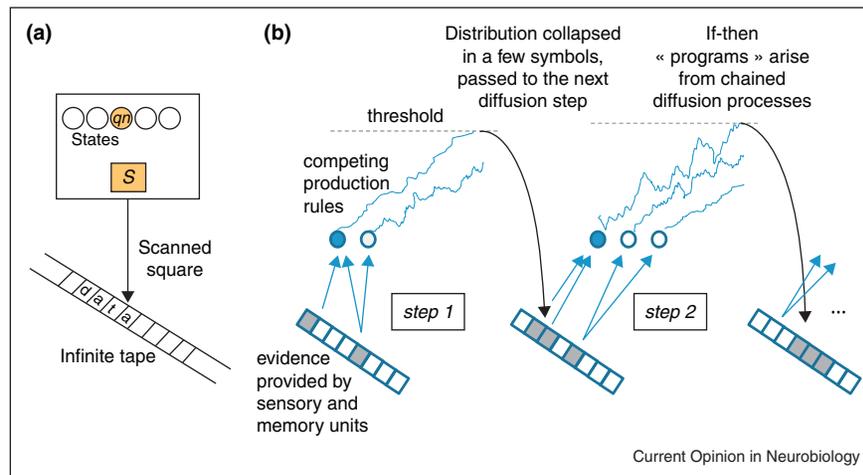
We have proposed a framework for the neural basis of serial computations that puts together Turing's two seminal contributions [4,5*]. Our framework (Figure 1) assumes that serial tasks (e.g. computing 23×14) are assembled as sequences of elementary decision steps, each involving a parallel competition between a subset of 'productions rules', implemented by pools of neurons that accumulate relevant evidence. When one of the competing pools encoding a production reaches a threshold, the race concludes and the production ignites. The consequence of the phasic ignition of a production might be an overt motor action, for instance moving the eyes towards a target, but also a covert effect, transiently changing the properties of a subset of cortical areas through an addressing mechanism [6]. This is equivalent to the action performed by a Turing machine in a single step: if a given condition is verified in the current memory state, it modifies the state of the memory, after which a new cycle begins.

This theory supposes that the circuits for sensorimotor decision making, instead of simply triggering motor actions, have been co-opted to implement a broader if – then logic. As noted by Shadlen *et al.* [7], "*the 25 million years of evolution between macaque and humans has probably served to expand the cortical mantle in the service of this nested intentional architecture . . . This seems far more likely to have occurred than the evolution of brand new principles of neural computation.*"

Here, we argue that the configuration of this process requires a distinctive control mechanism that conveys flexibility at the price of slow serial performance. Our framework envisages human rational thought as a combination of two elements: (1) A vast parallel machinery for decision making by accumulation of multiple sources of evidence, which contributes to intuitions, hunches, and a very rapid ignition of relevant actions; and (2) a capacity to link each of these decisions into 'strategies' or 'programs', where the outputs of one decision become the inputs of the subsequent decision, thus creating serial programs.

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Figure 1



A neurobiological framework for assembling serial decisions into a mental algorithm. **(A)** Alan Turing's formal machine [3] implements programs as a series of state-dependent conditional rewriting operations on an infinite tape. **(B)** The proposed framework for the neural basis of serial computations brings together the Turing machine and the evidence-accumulation scheme [4,29*]. We propose a sequential/parallel device in which each step involves the parallel competition between a subset of 'productions rules', implemented by pools of neurons that accumulate evidence up to a threshold. Once a production attains a threshold, probability distributions are collapsed in a few symbols (mean, variance, confidence) and passed to the next operation. The production can have overt effects (actions) as well as covert effects in modifying the state of the memory, after which a new cycle begins. In this architecture, each elementary step represents a complex massively parallel process of inference resulting in a single decision. Individual steps are analog in nature, but each is followed by a discretization step with a threshold. The latter mechanism provides control over the propagation of noise in analog computation, a problem stressed by John Von Neumann in his 1958 book 'The Computer and the Brain' [94].

Two theories on how the brain implements multiple decisions

Over the past years, Cisek, Kalaska, Shadlen and others have argued in favor of a parallel decision framework, and questioning the role of an executive system coordinating decision making. Their argument rests on the following observations. First, during a decision process, the same neuron may, at different times, encode stimulus properties, a decision signal, or a motor response [8,9,10*]. This argues in favor of distributed instead of centralized organization of decision variables. Second, when a monkey faces opposite actions that will be resolved after a delay, the monkey appears to prepare both movements simultaneously during the initial period of uncertainty, instead of storing target locations in a general-purpose working memory buffer [11].

However, we suggest that these data do not refute the influence of a central executive in the decision process. They merely argue against a naïve box-and-arrow implementation. During a single decision, the transfer from perception to decision and response is not strictly serial, but rather involves parallel computations and continuous flow [12] – a proposal with much support and a long history [13,14]. We argue, however, that a central executive plays an inescapable role in information routing, task setting, and task sequencing. This is manifest where patients with lesions of the executive system are unable to configure reliable decision paths [15,16]. Here we

specifically review data on multiple decisions, which consistently show that, whenever several decisions have to be articulated, a slow sequential organization is observed.

Evidence for serial operations in the human brain

A classical psychological observation, the *psychological refractory period* (PRP), illustrates the limits that human brain architecture imposes on parallel processing. When a human subject is asked to process two near-simultaneous stimuli as fast as possible, a striking seriality emerges: one stimulus is processed with no trace of interference, as if it was presented in isolation, but the response to the second is massively delayed, often by hundreds of milliseconds [17,18*,19–21]. This delay is observed even when, in principle, the stimuli and responses could be dealt with by independent brain systems or even by two distinct hemispheres [22,23]. It cannot be eliminated by training [24–27], even after thousands of trials [28*], suggesting that it reflects a structural bottleneck.

Response-time studies have refined the localization of the bottleneck, suggesting that sensory and motor processes can operate in parallel during the PRP, while a central response selection stage establishes a serial bottleneck [18*,19]. We have proposed that this bottleneck stage coincides with the noisy accumulation-of-evidence postulated in drift-diffusion models of decision making [29*].

This conclusion derives from the decomposition of response times into decision and non-decision components (see, e.g. ref. [30]). Only the experimental factors that influenced both the mean and the variance of response time (thus affecting the decision stage) also caused a delay that propagates to a concurrent task (thus affecting the central stage). In fact, the full, complex distribution of response times in a dual task could be explained by a model in which non-decision stages proceed in parallel, and only decision times are serially convolved [29*].

In event-related potentials (ERPs), the dual-task bottleneck relates to a late decision-related component referred as the P300. While subjects perform the first task, the early components of the ERP evoked by a second target T2 remain time-locked to T2 onset (and thus occur in parallel to T1-evoked activity), but the P300 is consistently delayed until after the T1 task is completed [23,31–34]. Time-resolved functional MRI [35] similarly indicates a delayed activation of a broad network including parietal and lateral prefrontal cortex [23,27,36–38]. This evidence is consistent with the proposal that in humans at least, even two seemingly unrelated decisions tie up a central executive or flexible routing system that is shared between many tasks [39–41].

For more complex tasks, there may be an even longer string of serial decision stages. For instance, when the participant chooses which task to perform first, response-time decomposition indicates a nested arrangement of *three* stochastic decisions [42]: Which task should I do first? What is the response to task 1? What is the response to task 2?

At even longer time scales, we predict that, during complex thought (e.g. mental calculation, internal speech, etc.), brain activity should organize as a long series of elementary decision steps. Because each step involves a noisy accumulation of evidence up to a threshold, the resulting activity should be dominated by noisy-triangular waveforms (periods of drift-diffusion interrupted by resets; Figure 1). Such activity may account for two properties that characterize spontaneous brain activity [43]: scale-free distribution (over a range of frequencies, power is distributed as $1/f^\beta$, with $\beta = 2$ for a Brownian diffusion process) and nested frequencies (in a triangular wave, power in the high frequencies is concentrated at specific phases of the lower frequencies).

Seriality and conscious control

Psychologists have long speculated that serial effortful performance is associated with the deployment of strategies that are consciously controllable and reportable [44,45]. Indeed, the parieto-prefrontal network that is tied during dual tasking overlaps strongly with the ‘global neuronal workspace’ postulated to underlie conscious

reportability [46*]. Furthermore, the mechanisms that lead to the postponement of the second task during the PRP are very similar to those that lead to the loss of conscious reportability during the attentional blink (AB) [[34], see also [38]]. In both cases, attending to a first target interferes with the central processing of a second one – in the PRP, by slowing it, and in the AB, by preventing it entirely. In both cases, early perceptual processing stages are intact, and only a late (>300 ms) stage is affected [34,47–50].

PRP and AB effects can even occur on intermingled trials of the same tasks [34,51], and the same variables are at play – for instance, slowing down the central stage of task 1 increases both the PRP and the AB [52,53]. Even the mere perception of an unexpected event [54] or the simple fact of becoming aware of a letter [55*], is sufficient to tie up central resources and create an attentional blink for an immediately subsequent stimulus.

If the central decision stage that is tied during serial processing underlies consciously reportability, then it follows that, during the dual-task delay, the second stimulus whose processing is postponed is not consciously perceived until it is centrally processed. This prediction was successfully tested [56,57]. During the PRP, human participants are capable of faithfully reporting their first response time, but not their second, nor even exactly *when* the second stimulus was presented [56]. This demonstrates that a tight relationship exists between central decisions and conscious reportability. It offers a potential explanation for why serial strategies require conscious perception (Figure 2; [58*,59]), and why we can accurately report our multi-step strategies, intermediate steps and subgoals, but not how we take an individual decision [45].

Chaining: a missing link

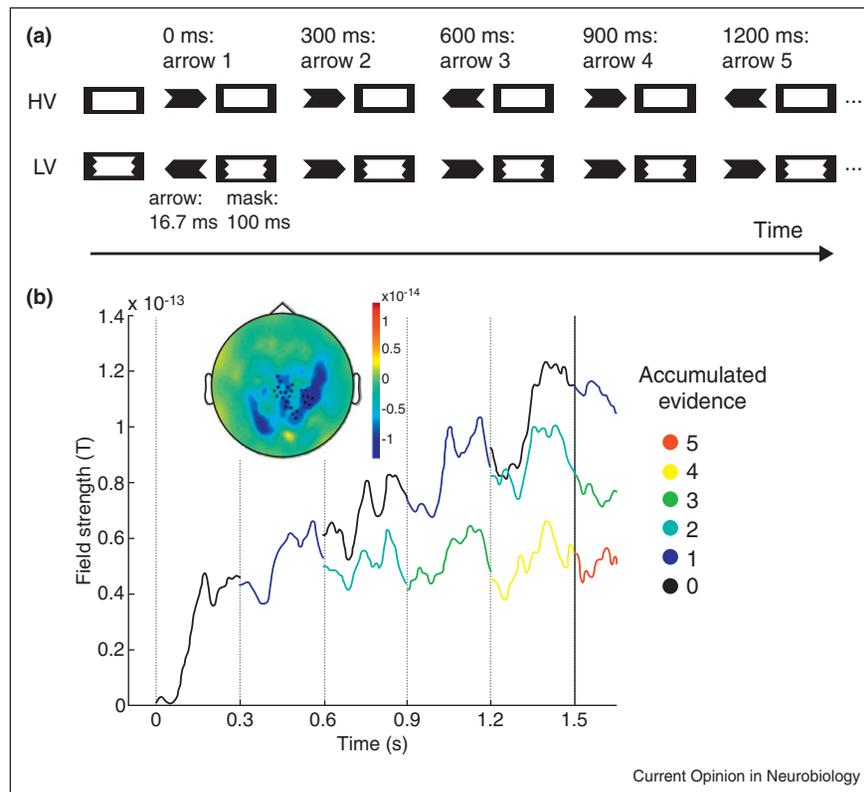
Of particular importance for building a mental program is the capacity to ‘chain’ operations, such that the output of the first one becomes the input to the second. Chaining is an understudied yet essential operation. It implies a flexible neural architecture for ‘routing’ information across any two brain processors, which is likely to involve prefrontal cortex [40,41,60,61].

Using behavioral response-time measurements, Fan *et al.* [62] demonstrated that in humans, even for identical tasks, stimuli and responses, chained operations are slower than independent operations by 60–70 ms. Thus, chaining corresponds to a measurable processing stage [see also [63]].

Two monkey electrophysiology studies suggest one possible mechanism for chaining: the maintenance of sustained activity in a relevant subset of neurons. Yang and Shadlen [64**] trained monkeys to make a saccade according to the total evidence provided by four

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Figure 2



A complex sequential decision task in humans. De Lange *et al.* [58*,59] asked humans to click left or right, according to the sum of evidence provided by five successive arrows, each of which could point left or right. The arrows could be masked down to near-invisibility (LV = low visibility), or they could be unmasked (HV = high visibility; panel A, from ref. [58*]). Behavioral findings revealed that, in both cases, decisions were based on an accumulation of the total evidence: subjects were increasingly fast and accurate as the number of arrows pointing to one side increased. Interestingly, when the arrows were visible, humans deployed a rational strategy of progressively lowering their attention as their running count of arrows increased, resulting in a decreasing amount of bilateral parietal activity with increasing evidence (panel B, from ref. [59]). When the arrows were masked, the participants no longer deployed this rational strategy, although their responses remained affected by an unconscious accumulation of evidence [58*]. The results suggest that conscious executive control may be needed to advance through a multi-step serial program [see also [63]].

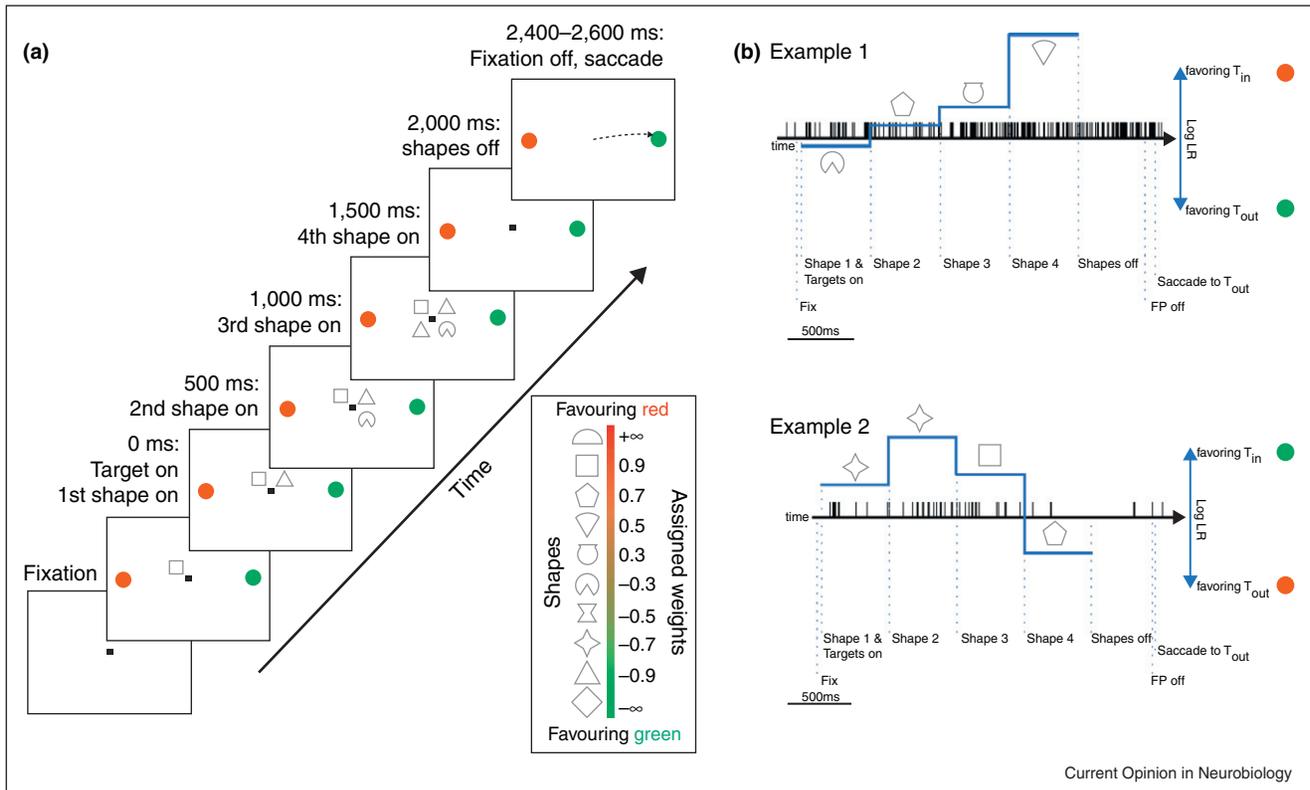
successive shapes (Figure 3). After each shape, the firing of LIP neurons was incremented or decremented by a roughly appropriate amount, suggesting that these neurons maintained a running count up to the final decision period (see Figure 2 for a similar task in humans). In the second study, capitalizing on previous demonstrations of serial curve tracing in human and non-human primates [65–68]. Moro *et al.* [69**] trained macaque monkeys in serial ‘search-then-trace’ and ‘trace-then-search’ tasks. Participants had to alternate between curve tracing and searching for a dot whose color matched the one found at a previous point (Figure 4). This series of purely mental operations was detectable as a sequence of precisely timed moments of amplified firing at the appropriate V1 locations [69**]. Thus, although retinotopic cortex is usually associated with early feedforward processing, it can also be recruited in a top-down manner during visual decisions [6,67,70,71] and maintain, via its sustained activity, a pointer to the current step in a series of decisions [69**].

Approximate seriality in a parallel brain

Unlike a digital computer, the brain only implements an approximate form of seriality. Not only do a variety of automatized perceptual and motor operations operate in parallel, but even central decisions may be occasionally subject to partial time sharing [72]. During the PRP, the response to the second item may interfere with the first, suggesting the presence of ‘cross-talk’ [22,23]. During curve tracing, the successive stages of amplification may partially overlap in visual cortex [69**]. During serial arithmetic, participants may start the second operation before finishing the first [63]. A decision may also continue after the motor response has been emitted [73], leading to error detection and ‘change of mind’ [74**].

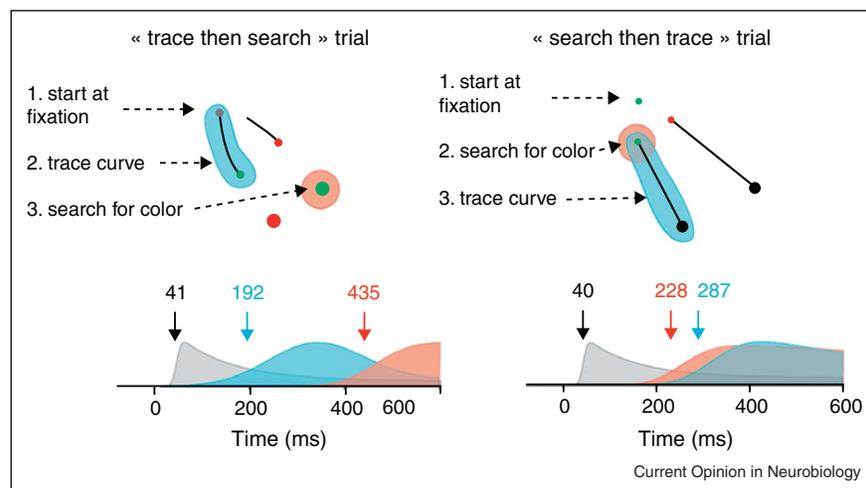
The human capacity for error detection and confidence monitoring suggests that even during a single decision, parallel hierarchical routes accumulate evidence at both motor and supra-motor levels [75]. In particular, the frontopolar cortex appears to implement a higher-order

Figure 3



A complex sequential decision task in monkeys. Yang and Shadlen [64**] trained monkeys to decide between a red and a green target. The task required summing the evidence provided by four successive shape cues of variable strength. Behavior and single-cell recordings in LIP revealed a prolonged phase of serial decision making associated with accumulation of the total evidence. The sustained firing of LIP neurons tracked the evidence accumulated to date at each time step. In the two example trials presented in panels B and C, the firing rate of an individual LIP neuron (spikes) can be seen to roughly covary with the total amount of evidence objectively provided by the successive shapes (blue square curve).

Figure 4



Evidence for serial operations in monkey area V1 [adapted from ref. [69**]]. Macaque monkeys were trained to perform a sequential task requiring successive covert operations of curve tracing and color search, in variable order, before making one saccade to the final target location. The left panel exemplifies a difficult 'trace then search' trial, the right panel a 'search then trace' trial. Below each trial type, curves show, as a function of time, the best-fitting solution of a mathematical model of the experimentally observed normalized multi-unit activity (arbitrary units; see ref. 69 for detailed methods). Gray: initial stimulus-induced response; Blue and red, additional response modulations observed when the traced curve (blue) or the searched color (red) fell inside the neuron's receptive field. V1 neurons whose receptive fields fell on the relevant path showed temporally ordered phases of amplification of neuronal activity, faithfully reflecting the order of the corresponding mental operations.

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meta-cognitive device that operates in parallel to the current decision, monitoring its success [76^{••}] and controlling the switch to subsequent steps [77–80].

Where is the program? Neural mechanisms for coordinating multiple operations

The precise mechanism by which the executive system organizes serial decisions remains unknown. We emphasize that we do not advocate a homunculus or any dedicated localized structure that will perform such a role. As a first step to understand how executive control is deployed over many parallel cortical processors, we modeled how a network of spiking neurons could implement a sequence of two independent tasks (Figure 4) [5[•]]. In the model, seriality in dual-task performance results as a consequence of inhibition within the control networks that impose a precise routing of information flow. The same structure that avoids spontaneous responses, perseveration, erroneous mappings, or responses to irrelevant stimuli results in a slow and serial sequencing of responses in dual tasks. Multiple sources of evidence are encoded in parallel and sustained transiently in meta-stable memory buffers. However, the ignition of productions that triggers the responses is strictly sequential and slow (~300 ms duration). This time constant is a consequence of the characteristic times of NMDA receptors and recurrent cortical circuits. Our architecture accounts in great quantitative detail for error patterns, response time distributions and brain activity patterns in a wide range of interference experiments such as iconic memory decay [81], masking [82], attentional blink [47,83] and psychological refractory period [19,37].

Concluding remarks

How the architecture of the brain supports multi-step operations remains largely unexplored. We conclude by pointing to two prominent challenges for further research.

First, dissecting the electrophysiological mechanisms of seriality is hindered by the intrinsic difficulty of training non-human primates in complex multi-step tasks. Indeed, such tasks tap rostral and mesial prefrontal cortical systems [77,84[•]] that are more expanded and connected in the human brain than in other primates [85–87]. Nevertheless, simplified animal models of human sequencing abilities can be developed and illuminate the neural coding of task sequences [88[•],89,90^{••},91,92].

Second, the brain may host serial programs, but not a programmer. The Turing-machine metaphor for the brain clearly breaks down here. Modeling studies are required in order to develop an understanding of how task-relevant sequences are assembled in prefrontal cortex, either by self-organization, through reward-based learning algorithms [40,93], or through linguistic instructions in humans [60].

Acknowledgements

Supported by INSERM, CEA, Collège de France, and an ERC grant 'NeuroConsc' to S.D. The authors are very grateful to Ariel Zylberberg and Mike Shadlen for stimulating discussions.

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