

RESEARCH ARTICLE

Recursion in action: An fMRI study on the generation of new hierarchical levels in motor sequences

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Abstract

Generation of hierarchical structures, such as the embedding of subordinate elements into larger structures, is a core feature of human cognition. Processing of hierarchies is thought to rely on lateral prefrontal cortex (PFC). However, the neural underpinnings supporting *active generation* of new hierarchical levels remain poorly understood. Here, we created a new motor paradigm to isolate this active generative process by means of fMRI. Participants planned and executed *identical* movement sequences by using *different* rules: a Recursive hierarchical embedding rule, generating new hierarchical levels; an Iterative rule linearly adding items to existing hierarchical levels, without generating new levels; and a Repetition condition tapping into short term memory, without a transformation rule. We found that planning involving generation of new hierarchical levels (Recursive condition vs. both Iterative and Repetition) activated a bilateral motor imagery network, including cortical and subcortical structures. No evidence was found for lateral PFC involvement in the generation of new hierarchical levels. Activity in basal ganglia persisted through execution of the motor sequences in the contrast Recursive versus Iteration, but also Repetition versus Iteration, suggesting a role of these structures in motor short term memory. These results showed that the motor network is involved in the generation of new hierarchical levels during motor sequence planning, while lateral PFC activity was neither robust nor specific. We hypothesize that lateral PFC might be important to *parse* hierarchical sequences in a multi-domain fashion but not to *generate* new hierarchical levels.

KEYWORDS

fMRI, hierarchy, motor, prefrontal cortex, recursion

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Significance Statement: Processing of hierarchical structures often activates lateral PFC, across several domains. However, it remains unclear whether this region supports the *generation* of new hierarchical levels, or other peripheral mechanisms supporting structure encoding and externalization components, such as motor execution. Using fMRI, here, we isolated (a) generative processes by inspecting the planning of identical motor sequences based on different (hierarchical and nonhierarchical) rules and (b) externalization processes by inspecting their execution. The generation of motor hierarchies via application of recursive hierarchical embedding rules was supported by a neural system used for motor imagery and planning. No evidence was found for lateral PFC involvement in the generation of new hierarchical levels. While lateral PFC might be important to *parse* hierarchical sequences in a multi-domain fashion, it might not be necessary to *generate* new hierarchical levels.

1 | INTRODUCTION

Much of what differentiates human behavior from that of other species is related to an increased ability to represent and generate complex hierarchies (Conway & Christiansen, 2001; Dehaene, Meyniel, Wacongne, Wang, & Pallier, 2015; Everaert, Huybregts, Chomsky, Berwick, & Bolhuis, 2015; Fitch, Friederici, & Hagoort, 2012). This is evident across several domains, including language (Chomsky, 1957) and music (Jackendoff & Lerdahl, 2006; Lerdahl & Jackendoff, 1977), but also actions (Fitch & Martins, 2014; Lashley, 1951). While animal behavior is for the most part serially structured, that is, can be described as a

sequence of movements in which each element (e.g., gesture) is maximally connected to one preceding and one successive element, humans can organize movements into superordinate clusters (Koechlin & Jubault, 2006), entailing several processing advantages. Humans, like other animals, use serial representations, for example, when we learn a motor sequence (e.g., a dance) involving multiple steps: $A \rightarrow B \rightarrow C \rightarrow D$. It frequently occurs that, when one step is forgotten (say C), we need to repeat the sequence from the beginning, because we are incapable of transitioning from B to D. This is because each node in the sequence is connected only to its adjacent successor but not beyond (Udden, Martins, Fitch, & Zuidema, in press). Hierarchy overcomes this limitation because individual behavioral units can be connected to more than one successor (or in hierarchical terminology, each parent node can be connected to more than one child). This allows elements in a motor sequence to be connected via a tree-like structure containing nonexpressed hidden nodes. For instance, take a procedure containing six steps $A \rightarrow B \rightarrow C \rightarrow D \rightarrow E \rightarrow F$ where two steps always form a structural unit $X[A,B]$, $Y[C,D]$, $Z[E,F]$. In a coffee-making procedure, X could be adding water to the machine (A. taking the pot out and B. pour water in it), Y adding coffee to the machine (C. get the coffee out and D. put coffee in the filter), and Z operating the machine (E. turn it on and F. turn it off). When we already put coffee in the filter the day before, we can easily transition from B to E because beyond the simple serial relations between steps (from A to F) we also represent the higher-level structural units containing these steps (X, Y, Z) and the connections between these units. This capacity to represent hierarchies seems to be particularly well-developed in humans, who can generate an unbounded number of hierarchical levels (Hauser, Chomsky, & Fitch, 2002) in a number of different domains.

Numerous studies in the domains of language, music, and vision have investigated the *discrimination* of hierarchical structures by asking participants to evaluate whether sequences of items are well-formed according to a previously learned system of rules (Bahlmann, Schubotz, & Friederici, 2008; Bahlmann, Schubotz, Mueller, Koester, & Friederici, 2009; Bianco et al., 2016; Friederici, Bahlmann, Friedrich, & Makuuchi, 2011; Maess, Koelsch, Gunter, & Friederici, 2001; Sammler, Koelsch, & Friederici, 2011). These studies suggest that lateral prefrontal cortex (PFC, particularly inferior frontal gyrus, IFG) might contribute multi-domain resources to the processing of hierarchies (Fadiga, Craighero, & D'Ausilio, 2009; Friederici et al., 2011; Patel, 2003), in interaction with areas along ventral visual/auditory streams that may store domain-specific schematic information (Bianco et al., 2016; Martins et al., 2014; Oechslin, Gschwind, & James, 2017; Pallier, Devauchelle, & Dehaene, 2011; Sammler et al., 2013). Recent anatomical research has shown that IFG in humans is expanded (Schenker et al., 2010) and more strongly connected with the posterior temporal regions in comparison to other primates (Neubert, Mars, Thomas, Sallet, & Rushworth, 2014; Rilling et al., 2008). If IFG supports the generation of hierarchies, these anatomical differences could explain why this ability is enhanced in humans. However, activity in this region across domains has also been argued to reflect general processes such as cognitive control and working memory, which might assist (but not be central to) hierarchical generativity (Fedorenko, Duncan, & Kanwisher, 2012; Matchin, Hammerly, & Lau, 2017; Novick, Trueswell, & Thompson-Schill, 2005).

In the present study, we went beyond *discrimination* and investigated the *generation* of hierarchically organized behaviors and their neurocognitive bases in the motor domain, where the generation of structures can be explicitly measured at the behavioral level. Previous research mostly relied on comparing classes of stimuli (hierarchical vs. nonhierarchical) that differ in their underlying generative rule system but also in their surface serial structure. This hampers the ability to separate processes involved in hierarchy generation from those involved in stimulus peripheral encoding. To solve this issue, our novel motor design experimentally separated generative act from execution: We asked participants to execute *identical motor sequences*, hence having identical surface structure, but to generate these sequences using *different rules*.

Crucially, the identical surface structure of the motor sequences could be represented as either being hierarchical or not. This enabled us to focus on the generative process, that is, in how far participants specifically represented a rule that generated new hierarchical levels versus a flat rule that merely transformed preformed hierarchies without generating new levels, and versus a mere repetition procedure without a transformation rule. As first rule, we used a recursive hierarchical embedding rule in which participants were required to generate connections between a parent node and a set of three children nodes (such as $X \rightarrow X[A1, A2, A3]$), thus generating a new hierarchical level. In the second rule (Iteration), successor elements were added serially, without generating new levels ($A1 \rightarrow A1-A2 \rightarrow A1-A2-A3$). Hence, these trials could be solved without representing cross-level relations. The third rule simply required to repeat the full sequence presented in a previous step condition, hence tapping into short term memory. The respective rule was revealed to the participants in a series of initial generative steps that they had to generalize to complete the trial with the correct motor sequence. We compared BOLD activity elicited by the use of recursive hierarchical embedding versus nonhierarchical iterative rules versus repetition separately during *planning* and *execution* of these motor sequences.

So far, behavioral and neural markers of action production have been extensively studied in contexts of (a) fast production of simple movement sequences without hierarchical relations (Elsinger, Harrington, & Rao, 2006; Hardwick, Rottschy, Miall, & Eickhoff, 2013; Héту et al., 2013) and (b) representation of hierarchical relations within action sequences but without active generation of new hierarchical levels (Fazio et al., 2009; Koechlin & Jubault, 2006).

The first stream of research demonstrated that learning to execute simple motor sequences is supported by a network including premotor and motor cortices (PMC and M1), superior parietal lobe (SPL), supplementary motor area (SMA), pre-SMA, left thalamus and right cerebellum (Hardwick et al., 2013). Furthermore, planning (keeping a given motor sequence in short-term memory) recruited a bilateral network comprising sensorimotor (M1S1) and premotor cortices, cerebellum and basal ganglia (Boecker, Jankowski, Ditter, & Scheef, 2008; Elsinger et al., 2006).

The second stream of research has focused on the neural bases of hierarchical action processing (when acts are encoded as parts of higher-order actions; Fazio et al., 2009; Koechlin & Jubault, 2006). These studies typically compare higher versus lower levels of given hierarchical action structures and have revealed posterior-to-anterior

activation gradients along lateral PFC with increasing hierarchy level. For instance, sequences of simple movements (left and right button presses) activate more anterior regions in lateral PFC when the movements are organized in superordinate clusters compared to when they are un-clustered (Koechlin & Jubault, 2006).

Overall, these studies provide neural evidence for (a) generative capacity but restricted to linear motor sequences and (b) hierarchical processing of actions, but without active generation of new hierarchical levels. Here, we combined these two approaches to go a step further and probe the mechanisms underlying the internally driven generation of hierarchically organized motor sequences.

Previous research on hierarchical representations in music, language or goal-directed actions (Fadiga et al., 2009; Fitch & Martins, 2014) points to the lateral PFC and IFG as a candidate region that may also be involved in the generation of new hierarchical levels in motor sequences, even though these studies did not isolate the *generative act* from the *processing* of given hierarchies. On the other hand, planning and imagery of complex motor sequences (independently of execution) are known to be supported by a motor network comprising M1S1, PMC, basal ganglia and cerebellum. In this study we will test whether the latter areas also support the generation of motor hierarchies, or whether this capacity requires dedicated systems in PFC hypothesized to support generation of hierarchies across multiple domains.

2 | METHODS

2.1 | Participants

Twenty healthy participants (11 males and 9 females, age range 21–35 years, $M = 26.5$) took part in the study. All participants were nonmusicians. None had more than 2 years of music training, and none practiced regularly with a musical instrument. All had normal or corrected-to-normal vision and audition, no history of neurological or psychiatric disease. All participants were right-handed German native speakers. Participants were recruited from a pool of subjects able to perform all behavioral tasks successfully (see below). They gave written informed consent before the experiment in accordance with the local ethics committee that had approved this study (016-15-26012015) and were paid 8 Euros/hour for their participation.

2.2 | Task and stimuli

Our approach involved the comparison of brain activity during active generation of motor sequences following two different rules – “Recursion” and “Iteration” – which can be used to generate or transform hierarchies (Hulst, 2010; Martins, 2012; Martins, Martins, & Fitch, 2015). A third rule – “Repetition” – controlled for simple action repetition and working memory without any transformation rule. This framework (discussed in detail in Fischmeister, Martins, Beisteiner, & Fitch, 2017; Martins, 2012; and Martins & Fitch, 2014) focuses on the contrast between “recursive hierarchical embedding” rules which can generate new levels at different subsequent steps and “iterative” insertions rules that do not. Importantly, our framework is orthogonal to

some previous formalizations (e.g., Formal Language Theory) which do not specifically target the difference between hierarchical embedding and linear operations (Martins, 2012, for a discussion).

Here, the “Iterative” rule adds items linearly within levels of a given hierarchy without generating new levels. For example, with the rule “add 1 B subordinate to A”, we can start from A[B] and, in the subsequent steps, generate A[BB], [A[BBB]], and so forth. Conversely, the “Recursive” rule allows the generation of new hierarchical levels at each following step. For instance, with the rule “add 2 α subordinate to α ” we start with “ α ” and generate the hierarchy “ $\alpha[\alpha\alpha]$ ” but also “ $\alpha[\alpha[\alpha\alpha] \alpha[\alpha\alpha]]$ ”, and so forth. These recursive principles can be described with a recursive notation $\alpha \rightarrow \alpha[\alpha\alpha]$, as in Lindenmayer systems (Lindenmayer, 1968). This kind of rewrite rules have been used to describe visual (Martins, Martins, & Fitch, 2016), melodic (Martins, Gingras, Puig-Waldmueller, & Fitch, 2017), and rhythmic fractals (Geambasu, Ravnani, & Levelt, 2016). To control for general task-effects involving visual-motor planning, working memory and movement sequence execution, our approach included a third rule – Repetition – in which complete motor sequences had to be repeated, without necessity to add any items or levels. This control task taxed the processes involved in acquiring, buffering, and executing a complete motor sequence.

In the motor task, participants were asked to produce sequences of finger movements that followed these rules on a keyboard with 16 keys: they had to press a correct set of keys in the correct order, and with the correct timing. The temporal structure (see Figure 1a) was given by an auditory metronome sounding at 240 bpm (four beats per second delivered through MR-compatible headphones). The typical trial was composed of three steps (I, II, and III) that unfolded according to one of the three rules: Recursion, Iteration, and Repetition (Figure 1b–d). In Steps I and II, participants executed the motor sequences by following visual cues appearing on the keys of a virtual keyboard displayed on the screen. The visual cues, used only in Steps I and II, were colored circles with different colors denoting the different fingers that participants had to use to press the keys (red: thumb, green: index, and blue: middle finger). The relation between Steps I and II revealed the underlying rule that participants had to apply in order to actively generate a final motor sequence in Step III without visual guidance and following the temporal structure (Figure 1a). Crucially, in the recursive rule, only the first two hierarchical levels were present at Step II, and participants had to generate a third level consistent with the previous ones. This required the simultaneous representations of the first two levels, and of the relations between them. In particular, each set of three keypresses $[K - 1, K, K + 1]$ at level $n + 1$ derived from a particular key K_n from which it was hierarchically dependent (see Figure 1d and caption for detailed illustration). The extraction of these cross-level relations was essential to generate Step III using the proper set of parameters.

The application of any of our three rules always generated a final motor sequence of the kind $[[[K - 2s, K - s, K], [K - s, K, K + s], [K, K + s, K + 2s]]]$. To increase stimulus variability, we introduced the changeable parameters s (contour) and K (reference key, which in the Recursive rule was also the initial key k_1). The parameter s could be a value within the set $\{-2, -1, 1, 2\}$. If s was positive (1 or 2), the

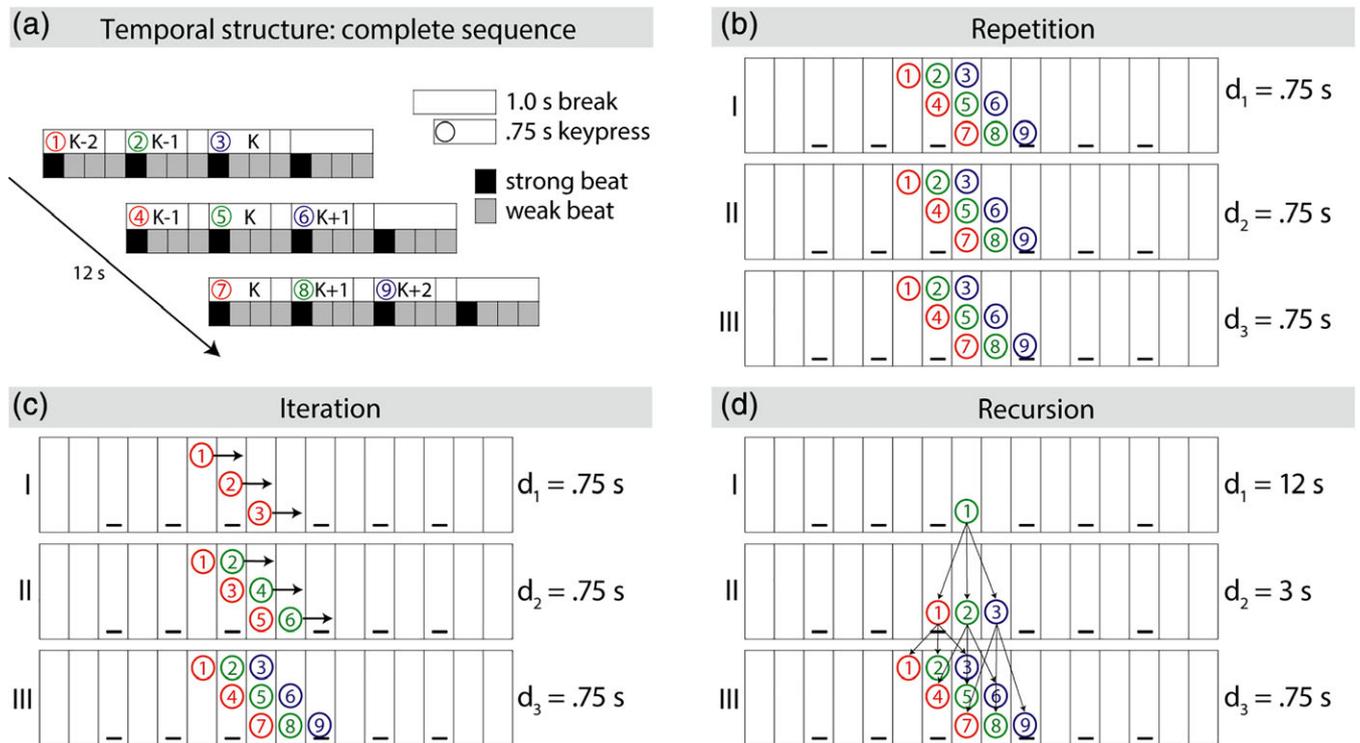


FIGURE 1 Task principles. In this task, participants were asked to generate sequences of 9 finger movements (ordered from 1 to 9) by pressing keys on the keyboard with the thumb, index, and middle finger (red, green, and blue). These sequences were formed in three Steps (I, II, and III) which followed one of three rules: simple Repetition (B), Iteration (C), and Recursion (D). During Steps I and II, participants executed the motor sequence guided by visual cues displayed on the screen. In Step III, they were asked to generate the final sequence of nine finger movements without visual support. (a) Temporal structure: In Step III, all rules resulted in the same complete sequence of 9 movements, grouped in three clusters, as here $[[K - 2, K - 1, K], [K - 1, K, K + 1], [K, K + 1, K + 2]]$, of 4 s duration each (total sequence duration = 12 s). K is the key in the spatial center of the pattern. Hierarchical clustering within the sequence (three clusters of three key presses) was given by the fingering pattern (red, green, and blue) and the temporal structure (1 s break after each cluster). To mark the temporal structure, the sequence was in fact aligned with a metronome with four beats per second (1 strong and 3 weak) with key presses starting on the strong beat and being released at the onset of the third weak beat (duration of each key press [d] of 0.75 s). (b) Repetition: consisted of the repetition of the complete sequence of nine finger movements three times. (c) Iteration: Step I was composed of three key presses executed with the thumb, each with $d = .75$ s, on the first (strong) beat of each cluster $[[K - 2, _, _], [K - 1, _, _], [K, _, _]]$. In Step II, a second key press with the index was added to each chunk: $[[K - 2, K - 1, _], [K - 1, K, _], [K, K + 1, _]]$. Thus, the iterative rule added elements to pre-existing hierarchical levels, without generating new levels. Step III was simply the serial completion of the pattern with the middle finger $[[K - 2, K - 1, K], [K - 1, K, K + 1], [K, K + 1, K + 2]]$. (d) Recursion: Step I was a single key press with the index finger (first finger, or 1) on key K with $d = 12$ s. Step II was a sequence of three key presses $[K - 1, K, K + 1]$ executed with the thumb (1), index (2), and middle finger (3), respectively, each with $d = 3$ s and 1 s break after each key press. The underlying Recursive rule was the substitution of each key press $a(k, f)_n$ (on key k and with finger f) in step n , with a sequence of three key presses $[a(k, 1)_{n+1} = a(k - 1, f)_n, a(k, 2)_{n+1} = a(k, f)_n, a(k, 3)_{n+1} = a(k + 1, f)_n]$, in step $n + 1$. In the time domain, each key press with duration d_n was substituted by three key-presses each with duration $d_n/4$ and followed by a break $d_n/12$. For simplification, we will refer to this rule as $k_n \rightarrow [(k - 1)_{n+1}, (k)_{n+1}, (k + 1)_{n+1}]$. Step III was obtained by applying the same transformation rule to each key press in Step II thus obtaining the complete sequence $[[K - 2, K - 1, K], [K - 1, K, K + 1], [K, K + 1, K + 2]]$. Each set of key presses at level $n + 1$ was clearly subordinate to one key press at level n . Therefore, the representation of the underlying hierarchical structure was a necessary condition to solve the task [Color figure can be viewed at wileyonlinelibrary.com]

sequences were *ascending*, meaning that they unfolded from left to right on the keyboard (e.g., $[K - 1, K, K + 1]$). If s was negative (-1 or -2), the sequences were *descending*, meaning that they unfolded from right to left on the keyboard (e.g., $[K + 1, K, K - 1]$). When $s = 1$ or -1 , the sequence (within each cluster) was formed by *adjacent* keys (e.g., $[K + 1, K, K - 1]$), and when $s = 2$ and -2 , the sequence was formed by *nonadjacent* keys, meaning that there was a space of one key between a pair of elements within the cluster (e.g., $[K - 2, K, K + 2]$). The reference key K (which is the spatial center to the pattern) could be one of the middle four keys of the keyboard $\{7, 8, 9, 10\}$. Overall, these variations

produced 16 different sequences, which were perfectly balanced across conditions. Crucially, parameters s and K had to be recognized during Steps I and II, in order to correctly generate the sequence in Step III.

2.3 | Pretest

All participants took part in a behavioral session up to 1 week before the fMRI experiment. The goal of this session was to instruct participants explicitly about the task rules, to assess their understanding of those rules and to train them in the execution of the motor sequences.

Note that none of the participants had experience in playing music, particularly not in playing on a piano. The session lasted approximately 2 hr. Participants started by performing a beat perception task (part of the battery used in Müllensiefen, Gingras, Musil, & Stewart, 2014), to evaluate whether they were able to understand the synchrony between two temporal events (a metronome and a music piece). Then, they were shown a slideshow explaining the task rules, and video examples with the motor sequences they had to perform (see Supporting Information).

After the instructions, participants performed a supervised session comprising 10 trials following the Recursive rule. They executed the sequences as depicted on the screen, that is, did not have to mentally generate the sequences by themselves, as Steps I, II, and III were all presented visually on screen (unlike in the task used in the MR scanner). A researcher was in the room supervising this session, incentivizing the participants to follow the temporal structure and to use the visual landmarks to find the correct keys. The goal of this phase was to train the participants with correct exemplars. We repeated this procedure for the Iterative rule.

If participants were able to execute the Recursive and Iterative sequences adequately, they proceeded to a final session, similar to the one used in the fMRI experiment. This session was composed of 20 trials including 8 trials following the Recursive rule, 8 trials following the Iterative rule, and 4 trials following the simple Repetition. In this last session, Step III was not cued visually, and participants had to generate the sequence by themselves, without visual support, but following the metronome, as later in the MR scanner.

Participants with accuracy >80% in the last session, for all rules, were invited to participate in the fMRI experiment. Accuracy was measured as the number of correct keys pressed at the correct time—within the interval $[-0.25\text{ s}, 1\text{ s}]$ locked to the onset of the appropriate beat. Each trial contained nine expected key presses in Step III. Twenty-one out of thirty-nine participants performing the pretest fulfilled this criterion. Note that, although only about 50% of our participants passed our selection threshold for the MRI experiment, those 50% were able to acquire a keypress accuracy above >80% after only 1 hr of training (roughly 64 trials). Despite the task being relatively difficult to learn in one training session, this is in line with previous research showing that more extensive training is necessary to reach adequate performance in simple, nonhierarchical motor tasks (Taubert et al., 2010; Taubert, Lohmann, Margulies, Villringer, & Ragert, 2011), and in artificial grammar learning in language (Opitz & Friederici, 2003). Recent behavioral data from our laboratory (unpublished) also suggests that more training, in terms of number of training sessions, increases keypress accuracy in our motor task.

In those participants who succeeded in the pretest, the “generation of new hierarchical levels” (i.e., in the Recursive rule condition) hence pertains to the application of well-learned hierarchical rules, independently on how these were acquired (Lungu et al., 2014). This may entail either the execution of *combinatorial computations* specifically involved in the generation of new hierarchical levels, or the *retrieval* of previously formed hierarchical representations (Figure 2), which remain stored as “schemas” within the motor network (Wiestler & Diedrichsen, 2013). Note that in case our task

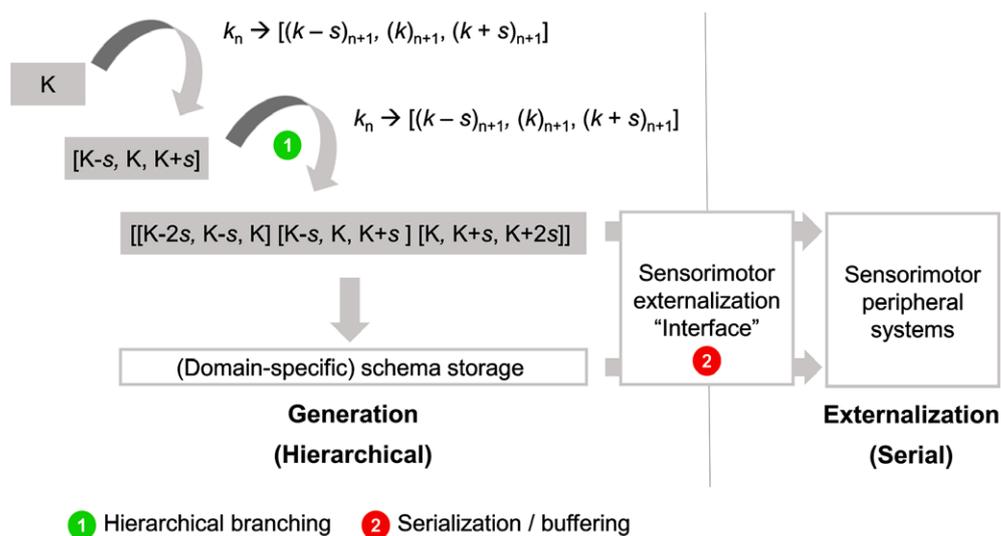


FIGURE 2 With our design, we explicitly separated the processes underlying the generation of hierarchical levels (left) from those used to externalize and execute motor programs (right). While the generation of new hierarchical levels in the Recursive rule involves hierarchical branching (left) and then serialization (right), Iterative completion of motor sequences is strictly serial. It should be mentioned that activations referring to the generation of new hierarchical levels can potentially involve either de novo combinatorial operations (upper cascade), or the retrieval of previously formed hierarchical representations (lower transparent box). The products of hierarchy-generating rules (e.g., $[[K - 2s, K - s, K] [K - s, K, K + s] [K, K + s, K + 2s]]$) might become schematized and stored in domain-specific networks from which they are retrieved during sequence generation. The schema would retain the clustered hierarchical structure and a set of free parameters binding different levels (in this study the reference key K , and contour variable s). Importantly, even if the latter were the underlying mechanism, participants would have to extract and apply the parameters from the second step of each trial, and obey the same hierarchically organized temporal cluster boundaries. Thus, irrespective of whether processing is based on combinatorial operations or retrieval of schemas, only recursion would entail flexible generation of hierarchical motor sequences [Color figure can be viewed at wileyonlinelibrary.com]

hinges on schema retrieval rather than on-the-fly generativity, these schemas are still not rigidly automatized: (a) they also entail a generative act since their internal spatio-temporal hierarchical organization needs to be constructed from the set of free parameters (s and K), and (b) the transformations within the Recursive rule are bounded by a hierarchical temporal clustering which is strictly scale invariant—that is, the key press duration at a subordinate level is exactly $\frac{1}{4}$ of that of a key press at the dominant level (Figure 1A).

2.4 | fMRI procedure

On the day of fMRI data acquisition, participants were again briefed on the task rules, then positioned in the scanner and asked to perform a short test session of six trials. If they were able to perform adequately, we proceeded with the anatomical and functional data acquisition. One participant was excluded due to inability to replicate the experiment within the MR experimental apparatus. At the end of the procedure, participants were given a questionnaire on their cognitive strategies used to generate Step III across the different tasks. The whole procedure (briefing, scanning, and questionnaire) had a duration of approximately 2:30 hr.

The fMRI scan included four sessions, each with an approximate duration of 15 min and composed of 20 trials—8 Recursion, 8 Iteration, and 4 Repetition trials. For the sake of maximizing the number of trials in the main tasks of interest, we kept the number of Repetition trials to half. Trials following different rules were inter-mixed within each session and pseudo-randomized. The trial sequence was determined using Optseq2 (<https://surfer.nmr.mgh.harvard.edu/optseq/>) to maximize the efficiency of fMRI signal acquisition.

Trial structure is depicted in Figure 3. We were interested in two periods within each trial, namely the transition between Steps II and

III—the *planning phase*—and in Step III—the *execution phase*. The *planning phase* was important to capture the computations necessary to transform Step II into Step III, and the neural systems instantiating these transformations.

The experimental apparatus is depicted in Figure 4. Participants performed the task while lying in the MR scanner, using a silent 16-key MR-compatible piano (Figure 4a). The keyboard contained visual and tactile markers on keys 3, 5, 7, 10, 12, and 14 (from left-to-right) for spatial reference (see Figure 1). We used a dual mirror system, so that participants were able to see both the virtual keyboard projected on the screen, and the physical keyboard on which they executed the motor sequences (Figure 4b). The position of the mirrors was adjusted individually for each participant. Both keyboards had visual markers on specific keys for visuo-spatial reference (Figure 4c). On the physical keyboard, these references could also be detected by touch. All participants used their right hand to perform the motor sequences.

2.5 | Data acquisition

The experiment was carried out in a 3.0-Tesla Siemens SKYRA whole body magnetic resonance scanner (Siemens AG, Erlangen, Germany) using a 32-radiofrequency-channel head coil. During the four sessions, functional magnetic resonance images were acquired using a T2*-weighted 2D echo planar imaging (EPI) sequence with TE = 30 ms and TR = 2000 ms. For each session, we acquired 450 volumes with a square FOV of 192 mm, with 31 interleaved slices of 3 mm thickness and 30% gap ($3 \times 3 \times 3$ mm³ voxel size) aligned to the AC-PC plane, and a flip angle of 90°. T1-weighted images for anatomical co-registration were either selected from the database of the institute or acquired using a 3D MP2RAGE sequence (TI₁ = 700 ms, TI₂ = 2,500 ms, TE = 2.03 ms, TR = 5,000 ms) with a matrix size of

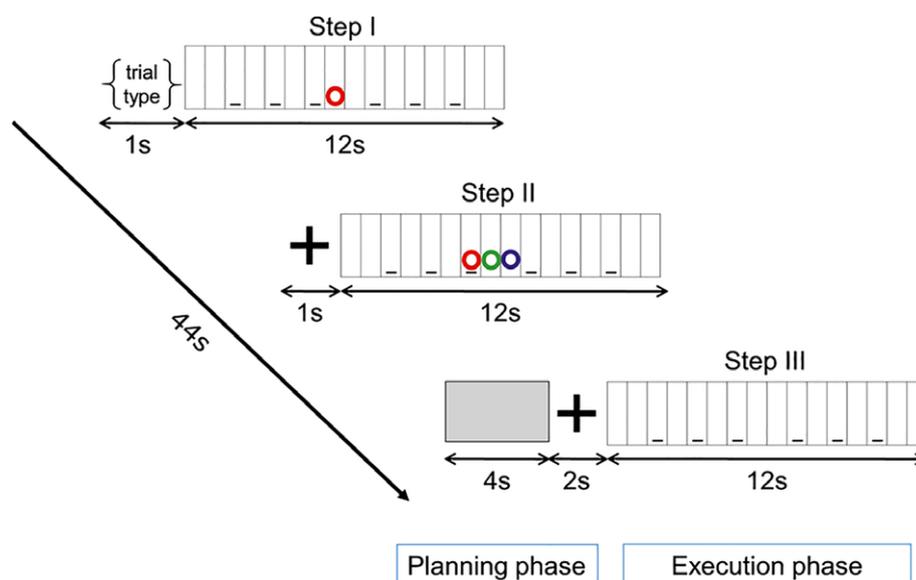


FIGURE 3 Trial structure (Recursion example). All trials had the same structure: First, a letter indicated the trial type. Then, Steps I and II of the sequence were shown on screen, which participants had to execute simultaneously on a keyboard (colored circles indicated which finger to use). This was followed by a 6 s *planning phase* composed of a 4 s blank screen and a 2 s crosshair during which participants planned execution of Step III. Finally, in the *execution phase*, participants performed the correct continuation of the sequence without visual cues. Throughout all steps, a metronome sound at 240 bpm guided participants' pace and the sequence's temporal structure [Color figure can be viewed at wileyonlinelibrary.com]

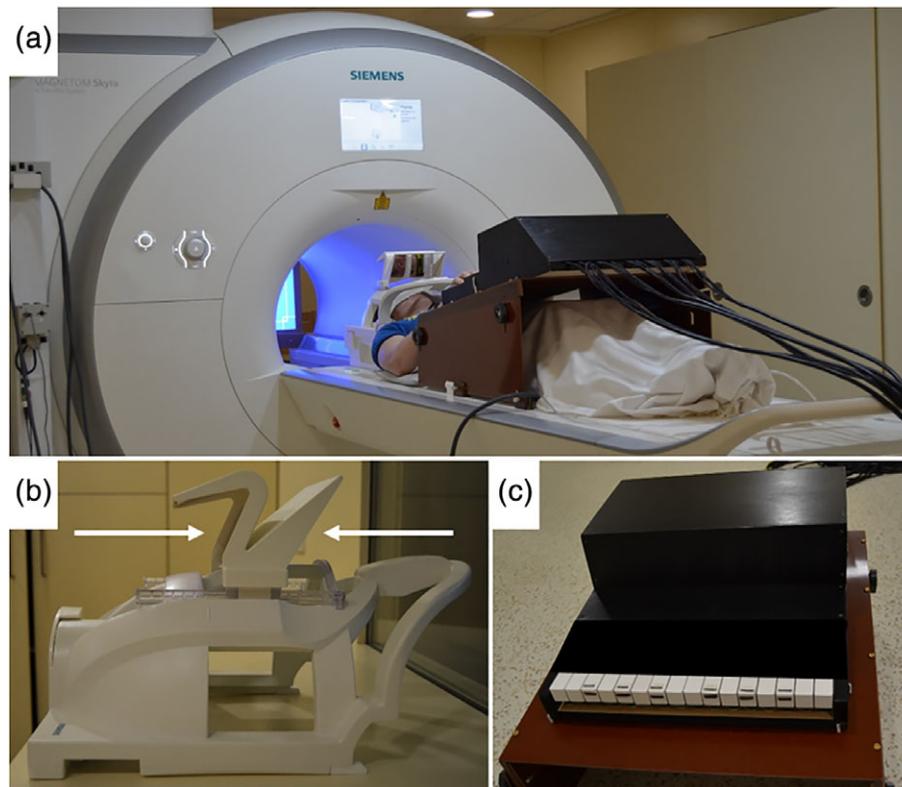


FIGURE 4 fMRI apparatus. (a) The keyboard was placed on a custom-made wood stand. This stand provided a degree of inclination that increased the visibility of the keyboard. The metronome sound was delivered through MR compatible headphones. (b) We used a double mirror system mounted on the head coil, which allowed participants to see both the virtual keyboard on screen (top mirror, left arrow), and the physical keyboard under their right hand (bottom mirror, right arrow). We adjusted the position of the mirrors for each participant to maximize visibility and comfort. (c) The keyboard was an adapted MR compatible piano in which the black keys were covered. We added visual and tactile cues on specific keys that the participants could use for reference. Importantly, pressing the keys on the keyboard did not generate any sound, and therefore key-tone associations could not be used in our task, which was purely visuo-motor [Color figure can be viewed at wileyonlinelibrary.com]

240 × 256 × 176, with 1 mm isotropic voxel size, flip angle₁ of 4°, flip angle₂ of 8°, and GRAPPA acceleration factor of 3.

2.6 | Data analysis

fMRI data were analyzed with statistical parametric mapping (SPM8; Wellcome Trust Centre for Neuroimaging; <http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>). Anatomical data from high-resolution T1-weighted images were obtained by masking the uniform tissue-contrast image with the second inversion image from the MP2RAGE sequence. Functional data were preprocessed by following standard spatial preprocessing procedures. They consisted of: slice time correction (by means of cubic spline interpolation method), spatial realignment, co-registration of functional, and anatomical data. Then, we performed spatial normalization into the MNI (Montreal Neurological Institute) stereotactic space that included resampling to 2 × 2 × 2 mm voxel size. Finally, data were spatially low-pass filtered using a 3D Gaussian kernel with full-width at half-maximum (FWHM) of 8 mm and temporally high-pass filtered with a cut-off of 1/128 Hz to eliminate low-frequency drifts.

Statistical parametric maps were generated for the whole brain data in the context of the general linear model (GLM). For each rule, we modeled three “trial phase” regressors at first level: (a) Steps I and II together, (b) planning, and (c) execution phase of Step III. This way

we could control for potential activity spill-over between phases. The evoked hemodynamic response to the onset of each phase was modeled for the Recursive rule, Iteration rule and simple Repetition conditions as boxcars convolved with a hemodynamic response function (HRF). We added estimated motion realignment parameters as covariates of no interest to this design to regress out residual motion artifacts and increase statistical sensitivity. Furthermore, we added two regressors to account for potential differences in difficulty between Recursion, Iteration, and Repetition: As a measure of *planning* difficulty, we modeled the average asynchrony between the first metronome beat (when participants should press the key) and the actual first key presses of Step III. As a measure of *execution* difficulty, we modeled the average asynchronies between the metronome beats and the actual key presses across all 9 key presses of Step III (mean response times for each key press are depicted in Supporting Information Figure S1). If participants pressed an incorrect or no key, we assigned the value 1 s, which is the highest possible value, that is, reflects maximal difficulty.

For random effects group analyses, two within-subject flexible factorial ANOVAs (with the factor RULE) were performed (for Step III *planning* and *execution*, separately) on whole brain data with binary gray matter masks thresholded at intensity value of 0.25. A main effect of RULE (Recursion, Iteration, Repetition) was detected in both

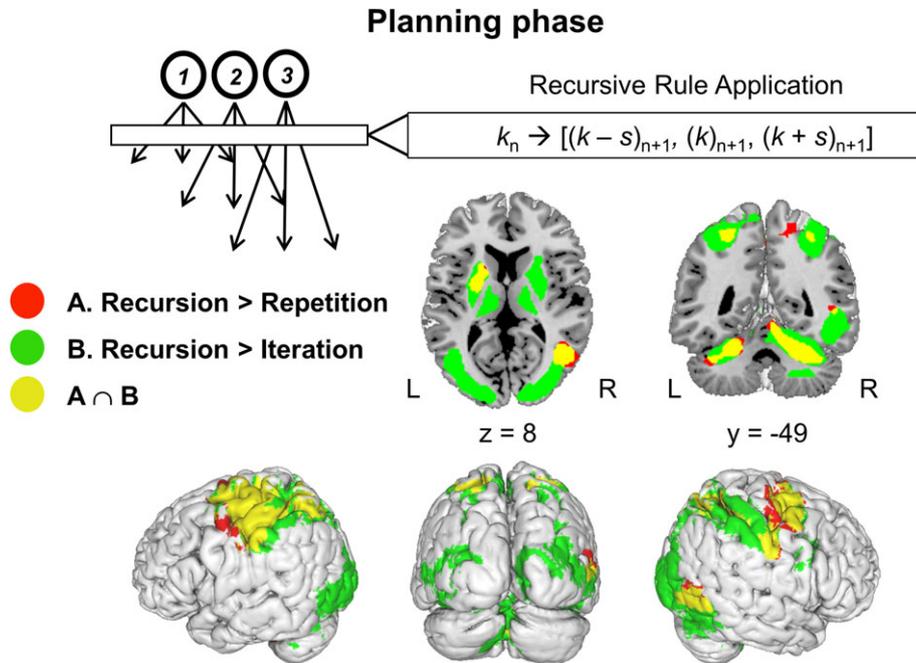


FIGURE 5 Brain activations during the planning phase (between Steps II and III). Application of the Recursive rule yielded stronger activations compared to both simple Repetition and Iteration in a bilateral network known to be involved in motor learning, planning, and imagery, including sensorimotor and premotor cortices, cerebellum, and lateral occipital cortex. The reverse contrasts (Iteration > Recursion and Repetition > Recursion) did not yield significant activations [Color figure can be viewed at wileyonlinelibrary.com]

planning and *execution* phases of Step III. To resolve these effects, statistical parametric maps with t-contrasts between each RULE were calculated. We controlled family-wise error rate (FWER) of clusters below 0.05 with a cluster-forming height-threshold of 0.001.

To test for the involvement of lateral PFC, particularly IFG, we performed small volume corrected (SVC) analyses within regions of interest (ROIs) comprising the left and right Brodmann areas (BAs) 44 and 45 based on the Harvard-Oxford probability maps (thresholded at 50%). Anatomical labels are based on Harvard-Oxford cortical and sub-cortical structural atlas implemented in FSL (<http://neuro.debian.net/pkgs/fsl-harvard-oxford-atlases.html>). In addition, we used REX toolbox (<http://web.mit.edu/swg/software.htm>) to extract the mean of the single-subject beta values across each ROI mask and calculated the t-contrasts between each RULE (Recursion, Iteration, Repetition), separately in the *planning phase* and the *execution phase*.

3 | RESULTS

In the present fMRI study, participants generated sequences of finger movements in three Steps (I, II, III) following one of three rules (Figure 1): (a) a linear Iterative rule, (b) a Recursive hierarchical embedding rule, or (c) simple Repetition. In the first two Steps (I, II) participants executed sequences guided by visual cues on the screen. Then, they were asked to generate Step III according to the respective rule without visual support (Figure 3). The fMRI analysis focused on the transition between Steps II and III, the *planning phase* reflecting the generative act, and on Step III, the *execution phase* reflecting the externalization. Importantly, motor sequences were identical in their surface structure across tasks. Hence, any difference in brain

activation during *execution* is likely to derive from the different outcomes of the generative phase.

Overall, we found that during action *planning*, the generation of new hierarchical levels in Recursion, compared to both Iteration and simple Repetition, yielded significantly stronger activity in a bilateral network of brain areas involved in motor planning and imagery (Hardwick et al., 2013; Héту et al., 2013), including M1S1 and PMC, cerebellum, lateral occipital cortex (LOC), and left putamen (Figure 5). Crucially, regions of interest (ROI) analyses within left and right IFG lent no evidence for involvement of lateral PFC in the generation of new hierarchical levels (Figure 6). In the *execution phase*, no activation was specific for Recursion (i.e., stronger than in Iteration and Repetition). Instead, execution of sequences formed by both Recursion and simple Repetition rules showed similarities when compared with Iteration in form of bilateral basal ganglia and thalamus activity (Figure 7). This suggests that other than *planning*, which required specific additional resources for Recursion, sequence representation during *execution* was not Recursion specific.

3.1 | Generation of new hierarchical levels is supported by general networks of motor planning

By measuring brain activity in the *planning phase*, we sought to identify neural networks underlying the cognitive processes that are relevant for the transition between Steps II and III, that is, the generative act as such. In simple Repetition, this process consisted in holding the full sequence of Step II in memory until its repeated execution in Step III (Figure 1B). In the Iterative rule, this process

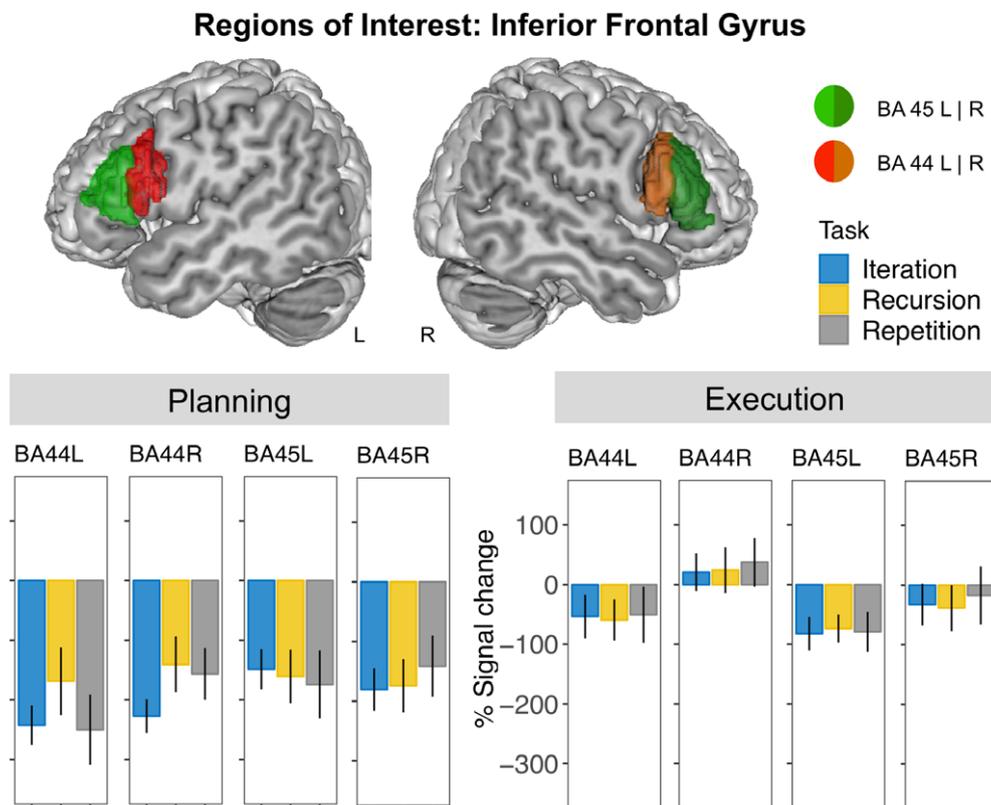


FIGURE 6 Global activity within the 4 IFG ROIs. Percent signal change (globally scaled) was higher in right BA 44 during *planning* in both Recursion and Repetition versus Iteration. However, this activity did not survive FDR threshold at $p < 0.05$. No significant differences were found during *execution* [Color figure can be viewed at wileyonlinelibrary.com]

required the serial addition of one key press to each cluster within a fixed hierarchical level (Figure 1C), without generation of new levels. The Recursive embedding rule entailed the generation of new hierarchical levels (Figure 1D) by recursively substituting each key press k_n in step n with a new sequence of three key presses $[(k-1)_{n+1}, (k)_{n+1}, (k+1)_{n+1}]$ in step $n+1$ (see Figure 1 for a detailed explanation). The parameters of the transformation rule to be applied in each trial's *planning phase*, s and initial key k_1 , could be inferred from the transition between Steps I and II (see Section 2 for details).

3.1.1 | Behavioral data

According to the postexperiment questionnaires (see Supporting Information Table S1), participants considered it equally difficult to extract the rule parameters in Recursion (mean \pm SD: 6.15 ± 0.88) and Iteration (6.40 ± 0.75 ; *Wilcoxon signed-ranks*: $z = -1.30$, $p = 0.19$), while it was easier to do so in Repetition (6.80 ± 0.41), than in the other two conditions (*Wilcoxon signed-ranks*: $z = -2.51$, $p = 0.01$, and $z = -2.13$, $p = 0.03$, respectively).

In addition, in Recursion trials, participants relied more on Step II for the generation of Step III (6.00 ± 1.52) than in both Iteration (5.20 ± 1.74) and Repetition (4.90 ± 1.75 ; *Wilcoxon signed-ranks*: $z = -2.35$, $p = 0.02$, and $z = -2.32$, $p = 0.02$, respectively). Finally, in comparison with Repetition, during Recursion participants (a) imagined more where the hand should go in key space, (b) prepared the sequence more consciously, and (c) thought more explicitly about

the rule (*Wilcoxon signed-ranks*: all $p_s < 0.05$). For detailed means and pairwise comparisons see Supporting Information Table S1.

To account for potential differences in task difficulty, we included the asynchrony between first metronome beat and first key press of Step III as a *planning* difficulty measure in our first level model (see Section 2). Averages of these asynchronies did not differ between tasks (Iteration: 0.30 ± 0.10 s; Recursion: 0.31 ± 0.09 s; Repetition: 0.30 ± 0.09 s; $F(2,38) = 0.14$, $p = 0.868$, $\eta_p^2 = 0.01$).

3.1.2 | fMRI

Whole-brain results of the *planning phase* are depicted in Figure 5 and Table 1. We found increased activity in Recursion in comparison with both Repetition and Iteration. The generation of new hierarchical levels in motor sequences using the Recursive rule was supported by a bilateral network known to be involved in motor learning (Hardwick et al., 2013), motor planning (Elsinger et al., 2006) and imagery of motor sequences (Héту et al., 2013). More precisely, this network included a large bilateral cluster with peaks in the cerebellum and extending through LOC, superior parietal lobe, M1S1 and left PMC (see Supporting Information Table S2 for more extensive enumeration and labeling of the peaks within this cluster). Further clusters included left putamen and pallidum, and right PMC (all clusters $p < 0.05$, FWE corrected). These activations were present in both contrasts Recursion $>$ Iteration and Recursion $>$ Repetition, and despite correcting for planning difficulty. Additionally, the contrast Recursion $>$ Iteration but not Recursion $>$ Repetition yielded stronger activation in right Pallidum and Putamen.

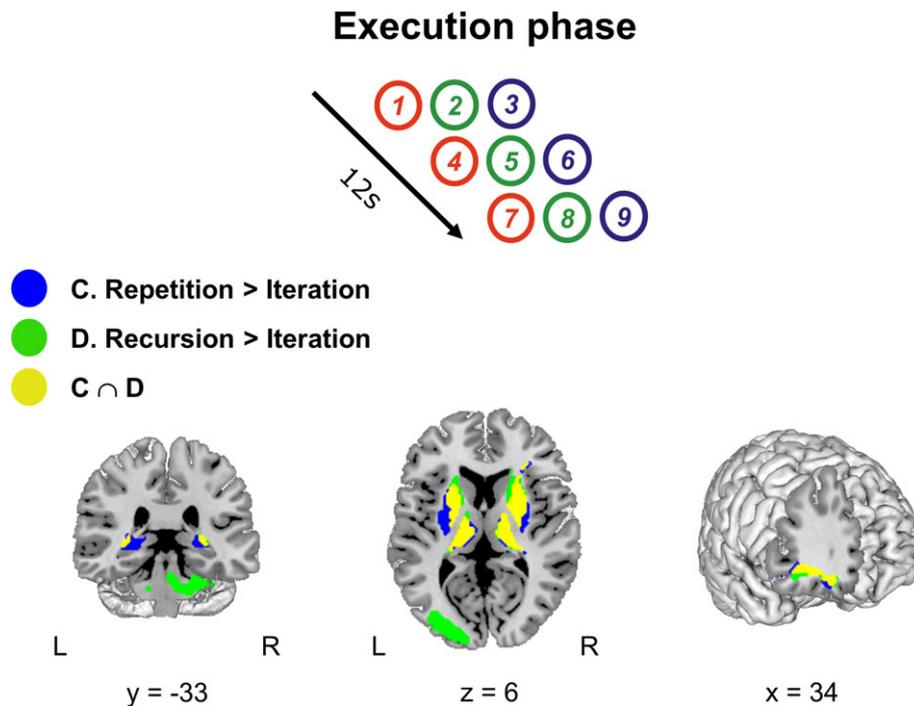


FIGURE 7 Brain activations during the *execution phase* (Step III). Participants executed sequences of nine key presses that were identical at the motor output but were generated according to different rules (Recursion, Iteration, and Repetition). Compared to Iteration, both Recursion and Repetition (C and D) activated the pallidum, putamen, and thalamus bilaterally. These clusters extended posteriorly into hippocampus and parahippocampus (left panel), and anteriorly into right orbitofrontal cortex (right panel; BA10 and BA47). In the contrast Recursion > Iteration we found an additional cluster in left LOC [Color figure can be viewed at wileyonlinelibrary.com]

Conversely, no activations were found for the Iterative rule or Repetition, that is, the contrasts Iteration > Repetition, Iteration > Recursion, and Repetition > Recursion did not yield significantly active clusters. Only Repetition > Iteration revealed activity in bilateral inferior lateral temporo-occipital cortex and frontal pole (Table 1), which may support mental practice and working memory for motor sequence (Jackson, Lafleur, Malouin, Richards, & Doyon, 2003).

3.1.3 | ROI analyses

To test whether there were specific activations for the Recursive rule within lateral PFC, particularly IFG, we performed four Small Volume Corrected (SVC) analyses within left BA 44, left BA 45, right BA 44, and right BA 45. Planned contrasts between rules yielded no significant differences (with uncorrected $p < 0.01$). The comparison of global activity within each ROI (see Figure 6) revealed stronger right BA 44 activity in both "Recursion > Iteration" ($T = 2.15$, p -uncorrected = 0.04) and "Repetition > Iteration" ($T = 2.41$, p -uncorrected = 0.02). However, these effects did not survive FDR threshold at $p < 0.05$.

We assumed participants engaged in specific computations to transform Step II into the final Step III in the Recursive condition, using an explicit motor-spatial rule. We found these specific computations were supported by general networks associated with motor planning and imagery but did not recruit IFG. The trend of greater activity in right IFG in both Recursion and Repetition versus Iteration suggests that these conditions may pose greater strain on working memory and motor control system (Aron, Robbins, & Poldrack, 2014).

3.2 | Execution of recursion- and repetition-based sequences (vs. iteration-based) recruits thalamus and basal ganglia

3.2.1 | Behavioral data

In the *execution phase*, sequences were motorically identical across all conditions. Importantly, key press accuracy did not differ between conditions (Recursion: mean \pm SD = 87% \pm 20%; Iteration: 89% \pm 18%; Repetition: 87% \pm 23%; generalized χ^2 score = 1.8, $p = 0.400$), suggesting that the execution was equally difficult. In addition, participants reported similar confidence in the correctness of their performance (regarding rhythm, keys pressed, and fingers used) in Recursion and Iteration (*Wilcoxon signed ranks*: p s > 0.400; see Supporting Information Table S1 for full details on means and pairwise comparisons).

Finally, we measured the asynchrony between metronome beats and key presses in Step III. Average asynchronies across the 9 key presses (Iteration: 0.21 \pm 0.13 s; Recursion: 0.24 \pm 0.14 s; Repetition: 0.30 \pm 0.12 s) did not differ between the three tasks ($F(2,38) = 1.27$, $p = 0.291$, $\eta_p^2 = 0.06$). To account for residual difficulty differences between tasks, we included the mean asynchronies for each trial as parameter into our fMRI statistical model.

3.2.2 | fMRI

In the *execution phase*, we found clear similarities between Recursion and Repetition that both dissociated from Iteration (Figure 7 and Table 2). We found significant activations in subcortical clusters including pallidum, putamen, and thalamus in both Recursion > Iteration and Repetition > Iteration contrasts. These clusters extended

TABLE 1 Effects of rule in the *planning phase*

Region	Hem.	BA	k	x	y	z	Z-value
<i>Recursion > Iteration</i>							
Cerebellum VI	R	-	23,865	26	-50	-30	5.97
		-		32	-42	-30	5.60
		-		8	-70	-34	5.44
Putamen	L	-	1,199	-26	-6	8	4.95
		-		-12	-18	2	4.79
		-		-24	-14	4	4.56
Pallidum	R	-	879	18	-2	0	4.71
		-		26	-8	10	4.67
		-		24	0	10	4.59
Precentral gyrus	R	6	1,108	42	-6	60	4.63
		6		24	-2	54	4.63
		6		32	-4	66	4.13
Brain stem		-	461	-6	-28	-22	4.01
		-		-4	-30	-30	3.69
		-		10	-26	-24	3.65
<i>Recursion > Repetition</i>							
Cerebellum VI	R	-	1,764	26	-52	-30	5.27
	L	-		-24	-50	-26	4.32
	R	-		32	-42	-30	4.10
Precentral gyrus	R	6	6,173	44	-6	56	5.00
	L	6		-24	-4	54	4.94
	L	3		-40	-20	54	4.85
Putamen	L	-	471	-20	12	-2	4.16
		-		-24	-4	6	3.93
		R		3	1,057	32	-32
Postcentral gyrus	R	2	1,057	54	-18	42	3.88
		2		40	-30	48	3.79
		R		V5	819	44	-62
Lateral occipital cortex	R	V5	819	52	-64	6	4.02
		-		34	-68	22	3.83
<i>Repetition > Iteration</i>							
Cerebellum I	R		2,466	48	-66	-22	5.31
				48	-56	-14	5.27
				26	-42	-42	4.75
Frontal pole	R	10	1,291	18	38	-16	5.22
		10		26	42	-8	4.63
		10		34	48	-4	4.36
Lateral occipital	L	V5	4,760	-42	-66	-10	4.81
	R	-		8	-70	-36	4.53
		V3		-28	-90	2	4.52
Occipital pole	R	V4	704	30	-90	2	4.42
		17		14	-94	12	3.87
		V4		38	-80	0	3.78

Whole-brain activation cluster sizes (*k*), MNI coordinates (*x*, *y*, *z*), and Z-scores for the rule contrast in the planning phase ($p_{\text{voxel}} < 0.001$; $p_{\text{cluster}} < 0.05$, FWE corrected). BA: Brodmann area; Hem.: hemisphere.

posteriorly into hippocampus and parahippocampus, and anteriorly into right orbitofrontal cortex (including BA10 and BA47). In Recursion > Iteration an additional cluster was found in left LOC. Finally, Iteration > Recursion did not yield significant activations that survived cluster level correction. However, one cluster in left primary somatosensory cortex (BA1) was significant with FWE-

correction at voxel level ($Z = 4.53$, $\text{voxel } p\text{-FWE} = 0.04$, $x = -50$, $y = -16$, $z = 48$).

3.2.3 | ROI analysis

Similar to the *planning phase*, we performed small volume corrected (SVC) analyses within IFG ROIs comprising left BA 44, left BA 45, right

TABLE 2 Effects of rule in the *execution phase*

Region	Hem.	BA	k	x	y	z	Z-value
<i>Recursion > Iteration</i>							
Pallidum	R	-	2008	16	-6	-6	5.53
		-		26	6	14	5.02
		-		22	14	10	4.69
Putamen	L	-	432	-22	4	14	4.95
		-		-22	12	12	4.73
		-		-22	-10	-4	3.86
Lateral occipital cortex	L	19	1,438	-30	-90	6	4.92
		19		-18	-94	-12	4.58
		18		-20	-94	8	4.29
Thalamus	L	-	1,117	-12	-6	2	4.17
		-		-26	-32	-32	4.03
		-		-4	-30	-28	4.02
<i>Repetition > Iteration</i>							
Pallidum	R	-	2,229	16	-6	-6	5.01
		-		26	0	14	4.69
		-		28	-28	-4	4.68
Putamen	L	-	1848	-24	4	12	4.61
		-		-10	-22	-18	4.48
		-		-22	-10	-4	4.26

Whole-brain activation cluster sizes (*k*), MNI coordinates (*x*, *y*, *z*), and Z-scores for the Rule contrast in the execution phase ($p_{\text{voxel}} < 0.001$; $p_{\text{cluster}} < 0.05$, FWE corrected). BA: Brodmann area; Hem.: hemisphere.

BA 44, and right BA 45. We found no significant differences between rules (with uncorrected $p < 0.01$). Global activity within each area was also not significantly different across rules (all uncorrected $p > 0.10$; Figure 6).

4 | DISCUSSION

To our knowledge, the present study is the first to investigate the neural systems involved in the generation and overt production of motor hierarchies, which clearly separates these two phases (generative act and externalization components). To do so, we developed a novel paradigm that contrasted (a) sequences of finger movements formed according to a hierarchy-generating Recursive rule with (b) identical sequences formed according to rules that did not require generation of new hierarchical levels (Iteration and Repetition). Each trial was composed of two initial Steps (I and II) that established the rules and a set of parameters which participants had to apply to correctly generate Step III. Thus, during *planning*, Repetition implied buffering of the given motor sequence $[[K - 2s, K - s, K] [K - s, K, K + s] [K, K + s, K + 2s]]$ and Iteration required the completion of a pattern $[[K - 2s, K - s, _] [K - s, K, _] [K, K + s, _]]$ using within-level transformations. Only the Recursive rule entailed the generation of new hierarchical levels through the recursive substitution of each finger movement k_n with a sequence of three finger movements $[(k - s)_{n+1}, (k)_{n+1}, (k + s)_{n+1}]$. Accordingly, participants reported mostly for the Recursive condition that they relied on Step II to consciously prepare the final sequence and imagined the sequence prior to execution. This entails that in the Iteration condition participants may have engaged less in active planning of Step III.

Nevertheless, Recursive and Iterative conditions did not differ in correctness of their execution or in subjective reports of general difficulty.

Our first important finding was that the generation (i.e., *planning*) of new hierarchical levels using the Recursive (compared to Iterative) rule was supported by a network of areas involved in motor learning, planning and imagery (Elsinger et al., 2006; Hardwick et al., 2013; Héту et al., 2013). This bilateral network included M1S1 and PMC, cerebellum, LOC, pallidum, putamen, and thalamus. Interestingly, in this study, which focused on the motor domain, we did not find evidence that these generative processes recruited IFG, an area thought to play an important role in the processing of hierarchies across domains (Fadiga et al., 2009; Fitch & Martins, 2014; Jeon, 2014). Although there was higher global activity within right BA 44 in Recursion compared with Iteration, this activity neither survived multi-comparison *p*-value correction, nor was it specific for Recursion, being present also in the Repetition > Iteration contrast. Therefore, right BA44 activity, if any, is not likely caused by computations specific to the generation of hierarchical levels using recursive rules.

Our second relevant finding was that *execution* of identical motor sequences generated by the Recursive rule or by simple Repetition of a given sequence, both involved bilateral subcortical areas including putamen, pallidum, and thalamus, extending posteriorly to hippocampus and parahippocampus, and in the right hemisphere anteriorly to orbitofrontal cortex, including BA47 and BA10. This suggests that identical sequences might be represented differently depending on their generative process. Notably, the similarity between Recursion and Repetition (vs. Iteration) suggests that these representations are

not specific to the processing of hierarchical relations, but to some other processes, which we discuss below.

According to the discrete sequence production framework (Verwey, 2001; Verwey, Shea, & Wright, 2014), performance involves (a) sequence generation and motor loading during planning, followed by (b) fast execution of the motor buffer content by effector-specific motor processors. The generation of new hierarchical levels in the Recursive rule puts particular strain on stage (a), the planning of the final sequence, by strongly relying on cortical resources. Unlike in Repetition and Iteration where the motor program is (partly) available already in Step II, performers have to use their rule knowledge in the Recursive condition to construct or retrieve motor schemas (see legend of Figure 2 about these alternatives) for appropriate sequence continuation. Interestingly, they seem to do so by means of general mechanisms of visuo-motor imagery and planning, as shown by stronger activity in bilateral visuo-motor networks (Hardwick et al., 2013).

Once formed, these motor programs are buffered in striatal areas and sent to the motor effectors for execution (Doyon et al., 2009; Miyachi, Hikosaka, Miyashita, Kárádi, & Rand, 1997). Our activity patterns in the *execution phase* speak for a similar buffering during Recursion and simple Repetition, but not during Iteration. Both Recursion and Repetition activated a fronto-striatal-thalamic circuit with the additional contribution of hippocampus/parahippocampus, and right orbitofrontal cortex (BA47 and BA10). The fronto-striatal-thalamic circuit supports motor control and working memory during sequence production (Humphries & Gurney, 2002; Schroll, Vitay, & Hamker, 2012; Vitay, 2010), and fronto-hippocampal areas have been associated with a global versus incremental representation of motor sequences (Lungu et al., 2014). According to these previous findings, we surmise that during production in both Recursion and Repetition conditions, a global representation of the full sequence is retained in working memory and used to optimize motor control, hence a correct motor sequence. It is very likely indeed that the sequence of nine finger movements was fully present during *execution*, being generated during *planning* in the Recursive condition (see paragraph above) and carried over from Step II in Repetition (see activity in right orbitofrontal cortex during planning). Conversely, during *planning*, we did not observe increased activity in Iteration in comparison with Recursion or Repetition. This may indicate less strain on the motor buffer, either because a sequence of only six finger movements had to be carried over from Step II to be linearly completed in Step III, or because participants used a generally different execution strategy that was less hinging on the motor buffer (although it fell short off significance at the cluster level, there was higher activity in left somatosensory cortex in Iteration during Step III than in Recursion). Overall, the results suggest that execution of a sequence formed by an incremental Iterative rule poses less demands on the motor control system compared to buffering and releasing the complete motor sequence in the Recursion and Repetition conditions.

In sum, we found that while generating new hierarchical levels in the Recursive rule demands more planning resources, serial completion of motor sequences in the Iterative rule might be achieved using sensorimotor areas during execution. Interestingly, these

additional planning resources in Recursion were instantiated by the motor imagery network, and they did not require IFG.

4.1 | Prior hypotheses: The role of lateral PFC/IFG

Based on current views that IFG is involved in the processing of hierarchies across many domains (e.g., language, music and action, as reviewed by Fadiga et al., 2009; Fitch & Martins, 2014; Jeon, 2014) and in line with models of a posterior-to-anterior gradient of lateral PFC for hierarchical organization of actions (Badre, 2008; Koehlin & Summerfield, 2007), we hypothesized lateral PFC, and particularly IFG, to support motor *generation* of new hierarchical levels in our Recursive rule condition. However, we did not find evidence for involvement of this area in the generation of new hierarchical levels. How can our results be reconciled with the previous literature?

On the one hand, the absence of evidence for lateral PFC activation in our task might indicate that this region is sensitive to hierarchies of action goals (or other nonmotor contextual dependencies; Badre, 2008), rather than to transparent rules describing cross-level relations in motor hierarchies (i.e., inducible without prior instruction) as tested in our task. Alternatively, the resources necessary to *discriminate* hierarchical sequences may not completely overlap with those used for the *generation* of new hierarchical levels, in that discrimination recruits numerous additional cognitive mechanisms that are not relevant during generation but may well account for IFG effects. For example, representing hierarchies from sequential input during *discrimination* also poses demands on resources required more generally for sequence encoding, buffering and template matching (Bornkessel-Schlesewsky, Schlesewsky, Small, & Rauschecker, 2015; Fitch & Martins, 2014), that may not be taxed to the same degree during the *generation* of hierarchical structures in the motor domain. Importantly, most discrimination studies found greater IFG involvement in material that drew strongly on these general resources, for example, by using sequences that were violations (Bianco et al., 2016; Molnar-Szakacs, Iacoboni, & Koski, 2005; Novick et al., 2005), had greater ambiguity (Rodd, Vitello, Woollams, & Adank, 2015; Vitello & Rodd, 2015), longer dependencies or posed higher demands on working memory than respective control sequences (Baddeley, 2003; Braver et al., 1997). This makes it difficult to dissociate the contribution of specific hierarchical generativity and general cognitive control/sequence encoding processes to the observed IFG activations (see also Fedorenko et al., 2012). Our design not only balanced the amount of required cognitive control across conditions (recall that final sequences were always correct, unambiguous and identical across conditions, although based on different rules); it also allowed us to study hierarchy processing stripped off general processes required for parsing temporally evolving sequences by specifically targeting hierarchy *generation* (in the planning phase). Consequently, the fact that we did not find evidence for lateral PFC involvement does not support the notion of multi-domain hierarchical generativity in IFG (Fadiga et al., 2009; Fitch & Martins, 2014) and rather argues for its more general function during encoding of structured sequences. It is important to note that while we did not find evidence for the role of IFG in the generation of hierarchies in the motor domain, this region could play a pivotal role in other domains such as language.

Since we focus on both *generation* of motor hierarchies (in contrast with, for instance, *processing* of linguistic syntax), we cannot draw strong conclusions about other domains. Although recent experiments in the music domain seem to suggest a similar absence of specialized IFG activity in the generation of new hierarchical levels versus serial iteration (Martins, 2017) further work is needed.

5 | CONCLUSION

In this study, we isolated the processes involved in generating motor hierarchies while separating them from other motor externalization components. Our results suggest that the generation of motor hierarchical structures via the application of recursive rules was supported by a neural system used for motor imagery and motor planning. Conversely, we did not find evidence that a putative multi-domain hierarchical processor in the lateral PFC is necessary for the generation of hierarchical levels in motor sequence production. While lateral PFC might be important to *parse* hierarchical sequences in a multi-domain fashion, due to encoding and externalization processes, it might not be necessary for the *generation* of new hierarchical levels.

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AUTHOR CONTRIBUTIONS

Mauricio J.D. Martins and Roberta Bianco contributed project conception, experimental design and setup, data acquisition and analysis, data interpretation, writing the manuscript; Daniela Sammler and Arno Villringer contributed supervision of the project, project conception, data interpretation, writing the manuscript.

DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author upon request. Authors can confirm that all relevant data are included in the article.

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