

Emergence of rhythm during motor learning

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Complex motor skill often consists of a fixed sequence of movements. Recent studies show that a stereotyped temporal pattern or rhythm emerges as we learn to perform a motor sequence. This is because the sequence is reorganized during learning as serial chunks of movements in both a sequence-specific and subject-specific manner. On the basis of human imaging studies we propose that the formation of chunk patterns is controlled by the cerebellum, its posterior and anterior lobes contributing, respectively, to the temporal patterns before and after chunk formation. The motor rhythm can assist the motor networks in the cerebral cortex to control automatic movements within chunks and the cognitive networks to control non-automatic movements between chunks, respectively. In this way, organized motor skill can be performed automatically and flexibly.

Control of serial order has long been thought to be the key to understanding a wide range of animal and human behavior including simple movements such as reaching, complex movements such as speaking, and logical reasoning [1]. This idea is now shared by many researchers who study the neural mechanisms of sequential movements [2–4]. How the brain represents and executes multiple movements in a fixed order has been and still is a formidable challenge to neuroscientists.

The actual performance of sequential movements is determined not only by the serial order of individual movements but also by their timing. The timing becomes a defining feature if the movement sequence has been so well learned as to be called motor skill. Sign your name on a piece of paper. You might notice that your hand and fingers move with a certain temporal pattern. As you repeat this task, an almost identical temporal pattern is reproduced [5], which can be called a rhythm. How does such a rhythm come about? There seems no obvious explanation. If your friends do the same task (i.e. sign your name), they will undoubtedly show different rhythms. Each of us produces a distinct signature pattern. Our unique motor rhythms appear to have emerged through repetition of the same sequential movements.

Although several recent studies have examined the properties of rhythm associated with motor performance [6–9], they were mostly concerned with externally guided

rhythms: subject were asked to synchronize movements to an externally presented rhythm or to remember and reproduce the rhythm. However, as in the examples mentioned above, the rhythms of our body movements can emerge spontaneously. We are not told to learn a specific rhythm and yet stereotyped rhythmic performance emerges nevertheless. This review focuses on such internally generated rhythms associated with performance of skilled movements. Interestingly, the rhythm that spontaneously emerges changes dynamically as we learn a sequential movement. We suggest that the change reflects restructuring of a long motor sequence into several short sequences or ‘chunks’. The motor sequence within a chunk can then be carried out automatically, which reduces the cognitive demand needed to control the performance of the entire sequence. The chunk pattern associated with rhythmic performance emerges spontaneously, but once established it becomes an inseparable component of skilled motor performance. We conclude that the rhythm of motor performance reflects a structured representation of the skill.

Reorganization of externally guided rhythm

Transformation of an unstructured rhythm into a structured form

Listen to a short phrase of a musical piece and then reproduce its rhythm by tapping your fingers. Here the rhythm of motor performance is externally guided. It has been shown that the accuracy in the reproduction of a rhythm depends on its interval ratios: a rhythm whose inter-tone intervals are related by non-integer ratios (1:2.5 or 1:3.5) or large integer ratios (1:5) can only poorly be reproduced in comparison with a rhythm related by small, integer interval ratios (1:2, 1:3, or 1:4) (Fig. 1a) [10,11]. Significantly, a non-integer rhythm tends to be transformed, during the learning or rehearsal of the rhythm, into one that can be related by small integer ratios. A rhythm with interval ratios of 1:2.5:3.5 tends to be reproduced as the one with interval ratios of 1:2:4 (Fig. 1a,b). A rhythm with interval ratios of 5:1:1 tends to be reproduced as 2:1:1 [12]. Such transformation occurs even when the instruction is to reproduce the original rhythm as accurately as possible [11] or not to consider the rhythm [12], so this process seems to be automatic and obligatory. Interestingly, the interval ratios

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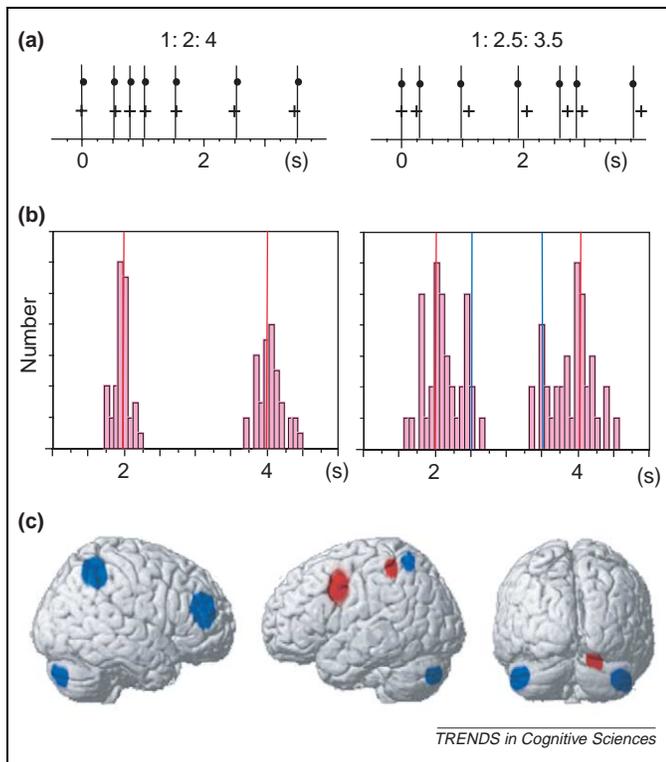


Figure 1. Behavioral performance of rhythm reproduction and neural representation of the rhythm. (a) Examples of a presented tone sequence (circles with vertical lines) and the sequence reproduced by a subject after a delay (crosses). Patterns are shown for a 1:2:4 rhythm (left) and 1:2.5:3.5 rhythm (right). Deviation of crosses from the vertical lines shows inaccurate reproduction of the more irregular 1:2.5:3.5 rhythm. (b) Histograms of the reproduced interval ratios for 1:2:4 (left) and 1:2.5:3.5 (right) rhythms. For the 1:2:4 rhythm, the peaks are found at 2 and 4 (red vertical lines), indicating accurate reproduction. For the 1:2.5:3.5 rhythm, the peaks should be found at 2.5 and 3.5 (blue vertical lines) but larger peaks are found at 2 and 4 (red vertical lines), indicating transformation of the 1:2.5:3.5 rhythm into a 1:2:4 form. (c) Schematic of the brain areas involved in the maintenance of 1:2:4 and 1:2.5:3.5 rhythms indicated in red and blue, respectively. The scans were taken during the delay period when subjects were rehearsing the presented rhythms. (a) reprinted with permission from [11].

of a freely generated rhythm are also shown to be either 1:2 or 1:3 [13–15].

A rhythm related with small integer ratios can be coded as a structured form, where each time interval is expressed as a multiple of a unit time and the entire series of the intervals is mapped onto a hierarchical structure [10]. By contrast, a non-integer rhythm cannot be expressed as multiple of a unit time and the series of time intervals is coded as a chain of independent, unrelated values. The rhythm remains unstructured and its maintenance is cognitively demanding. The tendency to re-code a non-integer rhythm into an integer rhythm might therefore reflect a self-organizing process to map the rhythm onto its closest hierarchical form and thereby to reduce the cognitive demand.

Neural mechanisms for processing structured and unstructured rhythms

Recent studies suggest that the processing of structured and unstructured rhythm is subserved by different neural substrates [11] (Fig. 1c). Maintenance of a structured rhythm is associated with activity in the premotor area and cerebellar anterior lobe, whereas maintenance of an unstructured rhythm is associated with activity in the

prefrontal cortex and cerebellar posterior lobe. As there are topographical connections between the cerebral cortex and cerebellum [16], this finding suggests separate motor and cognitive coding of structured and unstructured rhythms. This is in line with the idea of dissociation between automatic timing processes subserved by motor-related areas and cognitively controlled timing processes subserved by prefrontal cortex [7]. Automatic timing processes include performance of a well-learned rhythm [17], control of the acceleration and deceleration of a learned sequential hand movement [18], or synchronous tapping to the beat of a rhythm [19,20] especially as performed by professional musicians [8]. Controlled timing processes include encoding of time duration [21,22], explicit discrimination of time intervals [23], on-line adjustment of the timing of motor or cognitive action [19,24,25], or those in early phases of rhythm learning [26].

When subjects are presented with an unstructured rhythm but reproduce it as a structured rhythm, a shift of brain activation from cognitive to motor-related areas can be seen when the rhythm is transformed during rehearsal [11]. This can be viewed as a shift from controlled to automatic timing processes. A similar shift in brain activation from cognitive to motor-related areas is also observed when subjects switch from a syncopation mode to a synchronization mode when responding to an isochronous series of external stimuli [20,27–29]. Syncopated movements are thought to be performed as a series of independent movements that are planned and executed on each perception–action cycle. At a movement rate of 2 Hz or higher, syncopation becomes unstable and subjects spontaneously switch to synchronization [30] (but see [31]). This finding suggests a natural tendency for performance to shift from a cognitively demanding syncopation mode to automatic synchronization mode when a series of elementary movements is performed as a unitary sequence.

In short, a structured rhythm often emerges through reorganization of an unstructured rhythm. This reorganization is a naturally occurring process that reduces the cognitive demand, and involves a shift of brain activity from cognitive to motor-related areas.

Reorganization of internally generated rhythm

Emergence of a sequence-specific rhythm

When we type words using a keyboard, there is a stereotyped rhythm in the finger movements, especially for frequently used words or phrases. Here the rhythmic performance emerges spontaneously even though we are not told to move the fingers in a specific temporal pattern. When subjects learn a sequence of button presses with fixed response–stimulus intervals, longer reaction times (RTs) are observed at points in the sequence where there is a change in the pattern of finger movements, such as in repetition (for example, 123–123, where each number indicates the finger to be used), inversion (123–321) or transposition (123–234). The presence of longer RTs creates a temporal pattern specific to the sequence structure. For example, learning the sequence of finger movements, 123321456654123234345456 (where 1,2,3 indicate ring, middle and index fingers of the left hand,

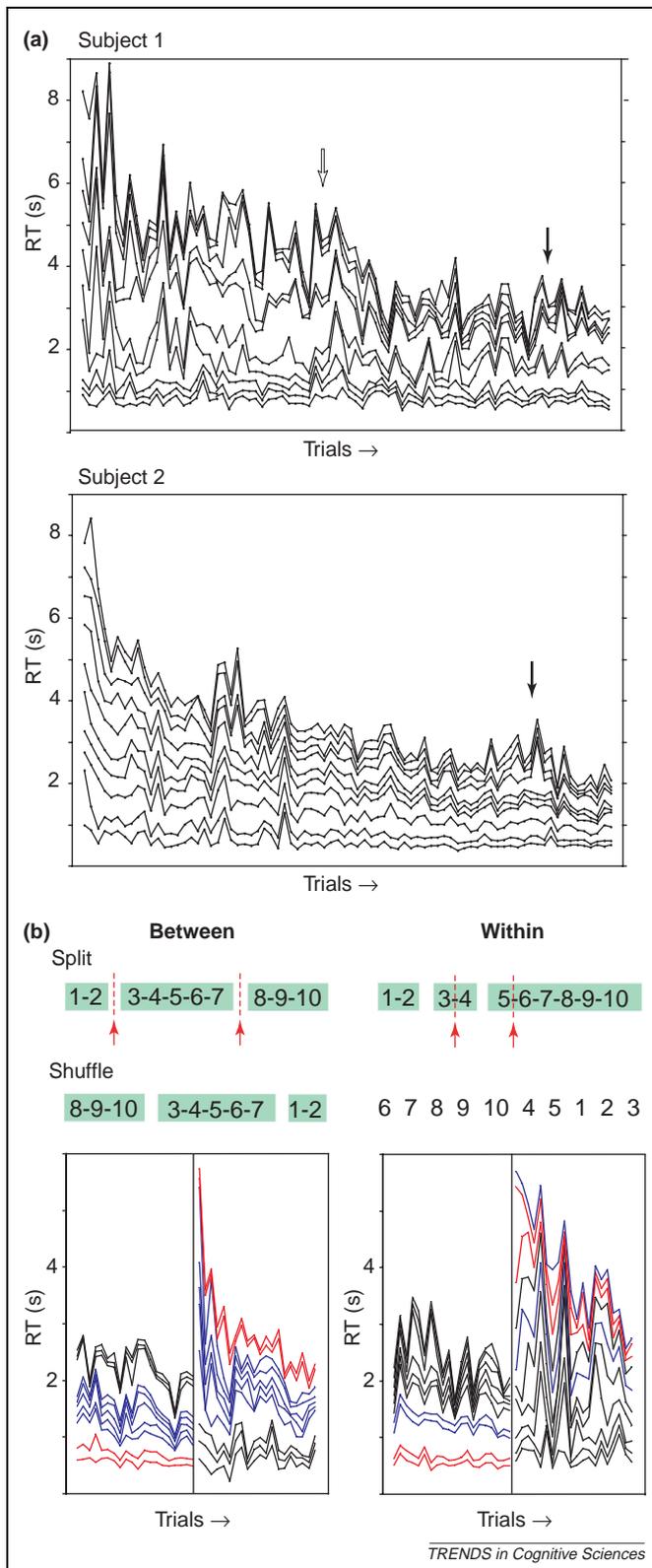


Figure 2. The learning of a sequence of 10 sets of two button presses. (a) Cumulative sums of the reaction times (RT) for the first button press of each set are plotted across the 10 sets (from bottom to top) over repeated performance (from left to right). The spacing between two adjacent lines corresponds to the time intervals between successive movements. Note the clustering of the lines as the number of trials increases, which indicates that the sequence is performed as clusters of sets, or chunks. The chunk pattern is different in the two subjects (compare Subjects 1 and 2, filled arrows), who performed the same sequence. It also changes during learning: Subject 1 performed the sequence as three chunks (12345-67-8910) in the middle of learning (open arrow) but at the later stage the pattern had changed to (123-45-678910) (filled arrow). (b) The split-and-shuffle procedure. A learned

sequence of 10 sets is split between- (left) or within- (right) chunks (red arrows and dotted lines). The split components are then shuffled to produce a new sequence of 10 sets. The two panels at the bottom show the cumulative sums of the inter-response intervals for the 10 sets, as in (a). The left half of each panel indicates the performance of the learned sequence, which shows clear chunk patterns indicated by grouping of red, blue and black lines. The right half of each panel indicates the performance of the shuffled sequence. Note the preserved chunk pattern and faster performance for the Between condition (left). There was no chunk pattern for the 'Within' condition (right) and the performance remained slow. (Subject 1 and (b) reprinted with permission from [38]. (a) Subject 2 is unpublished and is based on the data in [38]).

Emergence of a subject-specific rhythm

In the studies mentioned above the chunk pattern depends on the sequence structure, and therefore the rhythm of sequence performance is common across subjects. However a rhythm can emerge spontaneously in a subject-specific manner when there is no inherent structure in the sequence. In a recent study, subjects learned to press a sequence of 10 sets of two buttons using one finger [38]. There was no systematic repetition, inversion or transposition in the pattern of finger movements. As learning proceeded, the sequence of 10 sets was performed as 3-4 clusters of sets, which were separated from each other by longer RTs (Fig. 2a). In other words the sequence was reorganized into a hierarchical form composed of several chunks. Importantly, such chunk patterns in the advanced stages of learning differed across subjects even when they performed the same sequence, and the chunk pattern also changed during learning (Fig. 2a). In general there was a tendency for a sequence to be performed increasingly with fewer but larger chunks, which lead to a change in the rhythm with which the sequence was performed. The chunk points were associated with the subject's history of learning performance of the sequence. Another study has also shown the effect of prior practice for short sequences on the chunking pattern of a long sequence [39].

As this type of chunking emerges spontaneously, one might ask whether such chunking is in fact necessary for efficient processing of the entire sequence. This has been tested by the 'split and shuffle' procedure, that is, by asking subjects to learn a new sequence that is generated by shuffling the components of a learned sequence (Fig. 2b). The shuffled sequence was learned faster when the original sequence was split between chunks ('Between' condition) than when it was split within chunks ('Within' condition). This is because, when a chunk is preserved in a shuffled sequence, it can still be performed quickly as a

sequence of 10 sets is split between- (left) or within- (right) chunks (red arrows and dotted lines). The split components are then shuffled to produce a new sequence of 10 sets. The two panels at the bottom show the cumulative sums of the inter-response intervals for the 10 sets, as in (a). The left half of each panel indicates the performance of the learned sequence, which shows clear chunk patterns indicated by grouping of red, blue and black lines. The right half of each panel indicates the performance of the shuffled sequence. Note the preserved chunk pattern and faster performance for the Between condition (left). There was no chunk pattern for the 'Within' condition (right) and the performance remained slow. (Subject 1 and (b) reprinted with permission from [38]. (a) Subject 2 is unpublished and is based on the data in [38]).

single unit of action (Fig. 2b). A similar split and shuffle procedure has been used to analyze chunking by pigeons. Again the shuffled sequence is learned faster when the chunks in the original sequence are preserved, and the chunk is still performed as a single action when it is embedded in a new sequence [40].

Neural correlates for chunking

Recent studies have suggested that there may be specific neural mechanisms for chunking of a motor sequence. When monkeys learned a motor sequence consisting of five sets of two-button presses, at the beginning of learning, neurons in the pre-supplementary motor area (pre-SMA) fired before each set of movements, whereas after extensive learning the neurons fired only at the first set for the first few trials [41] (see also [42]). In the early stages of learning the chunk size was minimal – one set of button presses – so that the sequence comprised five chunks, whereas when the sequence was over-learned the entire sequence of five sets was represented as a single chunk. As pre-SMA neurons only fired at the beginning of a chunk, the learning-related decrement of activity in the pre-SMA seems to reflect the emergence of larger chunks to organize a sequence [41,43]. One possibility is that the pre-SMA plays a role in updating and loading of a new chunk. This hypothesis is supported by a recent study using transcranial magnetic stimulation (TMS) [44]. As human subjects learned a 12-move finger sequence, a subject-specific chunk pattern emerged. After extensive learning, inactivation of the pre-SMA by TMS affected the performance only when TMS was applied between chunks but not within a chunk. Inactivation of the premotor cortex did not affect performance of the sequence, regardless of the timing of TMS, indicating the specificity of the role of the pre-SMA in chunking. It has also been shown that, in monkeys, acquisition of new sequences but not execution of well-learned sequences is affected by inactivation of pre-SMA [45].

Whereas processing within a chunk is carried out automatically, processing beyond the boundary of chunks requires selection of the next chunk [46]. This is carried out by a cognitive control system, possibly mediated by the prefrontal cortex through pre-SMA. The learning-related reorganization of a sequence by increasing chunk size reduces the demand of cognitive control and results in a shift of brain activity from cognitive areas, such as the prefrontal cortex [43] and pre-SMA, to areas more related to motor execution, such as the supplementary motor area proper [41,45,47] and primary motor cortex [48–50]. It is unknown whether the chunking of non-motor items involves similar neural mechanisms (Box 1).

In summary, the rhythm of sequence performance is not intentionally learned but emerges spontaneously through restructuring, or chunking, of the motor sequence. The rhythm is not a by-product of sequence performance but rather reflects the sequence organization at a representational level. Once the rhythm has been established, it becomes an inseparable part of sequence performance. One can perform the learned sequence with a different rhythmic pattern but this requires cognitive control.

Box 1. Other types of chunking

Chunking strategy is widely used to remember a series of items. We usually remember a phone number as a series of two or three chunks. The postcode in the UK is explicitly designed to induce chunking by using letters and numbers (e.g. NW3-1NH). The chunk pattern can create a rhythm in verbal sequences. Its importance is highlighted by prosody (pauses, emphasis, pitch etc.), a mode of human communication that is not captured merely by the sequence of words. One type of traditional Japanese short poem, the 'haiku', is formed with a pattern of 5–7–5 phonemes, which creates a stereotyped rhythm when read aloud. Similar rhythms composed of 5 and 7 phonemes are also used in the lines of 'kabuki' players and can convey powerful emotions and connotations.

Chunking strategy is also used in remembering a sequence of spatial locations. When the sequence contains familiar shapes, such as right angled triangles and parallelograms, the performance is better than when the sequence has less symmetry and fewer parallel sides [65]. Multiple spatial positions are reorganized into higher-level groups or chunks.

Brain imaging studies have shown that the prefrontal cortex is involved in chunking of verbal and spatial sequences [65,66]. This area is thought to play a role in transformation of a perceptual code to a motor code, possibly by sending control signals to posterior areas [67]. It could be that a shift of brain activity from cognitive to motor-related areas also occurs during these types of chunking.

Chunking can occur even when there is no sequence information. For example, chess masters are shown to remember the positions and identity of multiple chess pieces as a single entity, which gives them recognition memory three times better than amateur players [68]. Thus, chunking is generally a strategy to code multiple items in a relational structure. It is an open question whether similar neural mechanisms underly the formation of non-sequential perceptual chunks and sequential motor chunks.

A stereotyped rhythm is the cardinal feature of automatic sequence performance.

A shift from controlled to automatic processing within a parallel neural network

Whereas learning a rhythm requires processing of temporal information alone, learning a motor sequence requires processing of spatial information. Are the processing of temporal information and the processing of spatial information independent? Recent studies have shown that, when temporal processing and spatial processing are done explicitly, they are associated with separate neural structures. Specifically, the cerebellar posterior lobe is involved in processing of temporal information whereas the pre-SMA or parietal area is involved in processing of spatial information [6,24,51,52]. However, a controversy remains as to whether the cerebellum is the area dedicated specifically to temporal processing [53,54]. It also remains unclear whether other cognitive processes that involve the cerebellum can be explained in terms of timing. Integration of temporal and spatial information is shown to be carried out within motor-related areas, including the lateral premotor cortex [24,51,52]. It remains controversial whether or not implicit learning of the two types of information can occur independently [55,56].

Figure 3a describes our hypothetical model, in which each of the temporal and spatial circuits can operate in either a controlled or automatic processing mode. The cerebellar posterior and anterior lobes are hypothesized to subserve controlled and automatic processing of temporal

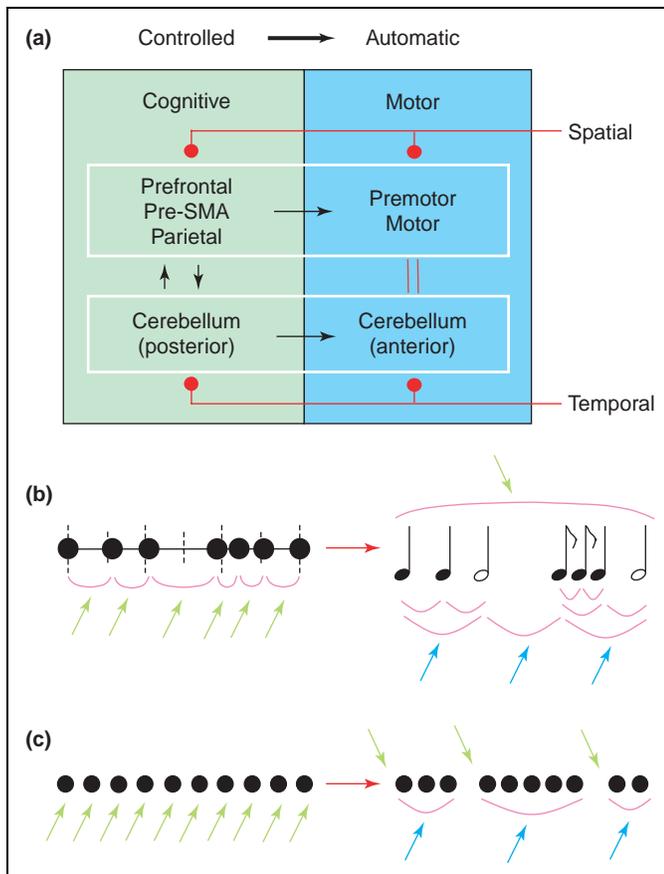


Figure 3. Hypothetical model of rhythm and motor skill acquisition. **(a)** Learning a motor skill involves a shift of processing mode from a controlled mechanism (green) to an automatic mechanism (blue). Spatial and temporal components of the movement are initially processed separately within cognitive neural structures. As the movement is learned the two components are integrated within the motor related structures. **(b)** In remembering an unstructured rhythm, controlled processing initially predominates to maintain each of the time intervals of the rhythm (green arrows). The rhythm cannot be mapped onto a hierarchical frame (vertical broken lines). After restructuring of the rhythm into a hierarchical form (chunks), each element of the rhythm can be processed by the automatic mechanism (blue arrows). **(c)** A motor sequence is initially performed by the controlled mechanism which operates on each elementary movement (green arrows). After learning the sequence is organized into chunks of short sequences, each of which is performed by the automatic mechanism (blue arrows). The controlled mechanism operates only at the beginning of each chunk.

information, respectively. Cognitive and motor-related areas in the cerebral cortex are hypothesized to subserve controlled and automatic processing of *spatial* information, respectively. Transformation of a rhythm into a structured form (Fig. 3b) involves a shift of brain activity from cognitive to motor areas in the cerebellum. Learning-related reorganization of a motor sequence into a hierarchical structure (chunking; Fig. 3c) involves a shift of brain activity from cognitive to motor-related areas in the cerebral cortex. It is an open question whether the cerebellar contribution to motor sequence learning is related to chunking [47,57] (see also Box 2 for other future research questions). The shift of activation from the posterior cerebellar lobe to the anterior lobe is also observed during learning how to use a computer mouse with a novel rotational transformation, a skill that does not involve learning a specific sequence [58]. A learning-related transition from controlled to automatic mode has been proposed previously by Fitts [59] and Anderson [60], and a recent model has stressed the parallel mechanisms

Box 2. Questions for future research

- What is the difference in the neural mechanisms underlying emergence of an internally generated rhythm and learning of an externally imposed rhythm?
- Why do freely generated rhythms always have interval ratios of 1:2 or 1:3?
- What kind of neural computational mechanisms in motor-related areas represent hierarchical structures?
- To what extent can spatial and temporal processing be separated in representation of motor skill?
- What are the similarities and differences in the mechanisms of perceptual and motor chunking?

between the two modes of processing [2,61]. We suggest that automatic mechanisms for motor performance operate from the beginning of learning but predominate at later stages.

When movements become skilled, the temporal and spatial circuits operate in an automatic mode within motor-related areas. At this stage, the spatial and temporal components seem to be represented in a unified structure. For example, in handwriting a letter, the ratios of the time and space intervals between segments of the letter are preserved independently of the total time taken to write the letter, and of the size of the writing [5]. The unified structure in space and time might be a cardinal feature of motor skill, although different neural mechanisms have been shown to operate in continuous movements such as handwriting, compared with discontinuous movements such as sequential button presses [62]. Any sequential motor performance is discontinuous at the beginning of learning. As learning proceeds, sequence performance becomes smooth and continuous (e.g. as in handwriting). Learning-related changes in brain activation may be associated with the shift from discontinuous to continuous performance, which is achieved by chunking.

A recent review has distinguished three components of temporal structure necessary for fluent action performance; sequence preparation, velocity scaling, and timed anticipatory response [63]. It was proposed that these processes are subserved by the prefrontal cortex, basal ganglia, and cerebellum, respectively. This view is consistent with our present and previous models for the role of the prefrontal cortex and cerebellum [3,64]. The difference is that, in our model, the basal ganglia mediate reinforcement signals for the acquisition of correct performance rather than rapid performance.

Summary

Skillful performance of sequential movements is often rhythmic. The rhythm reflects chunking of the sequence into shorter sequences of movements. This chunking occurs spontaneously and differs between subjects. Behavioral experiments have shown that performance is more automatic within a chunk than between chunks. This suggests that automatic performance is acquired separately for sub-parts of the sequence. The emergence of a chunk pattern might be organized by the cerebellum, and human imaging studies suggest that the cerebellar posterior lobe contributes mainly to the non-rhythmic

temporal pattern before chunk formation, whereas the anterior lobe contributes to the organized rhythmic pattern after chunk formation. In cooperation with the cerebellar lobes, the cognitive and motor networks in the cerebral cortex are hypothesized to govern non-automatic and automatic movements, respectively. We speculate that rhythm facilitates motor-skill learning by achieving automaticity for serial chunks of movements, rather than for the entire sequence at once. Furthermore, chunking might provide a window onto the cognitive processes that guide or, conversely, interrupt otherwise automatic performance.

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