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Sequential learning in non-human primates

Christopher M. Conway and Morten H. Christiansen

Sequential learning plays a role in a variety of common tasks, such as human language processing, animal communication, and the learning of action sequences. In this article, we investigate sequential learning in non-human primates from a comparative perspective, focusing on three areas: the learning of arbitrary, fixed sequences; statistical learning; and the learning of hierarchical structure. Although primates exhibit many similarities to humans in their performance on sequence learning tasks, there are also important differences. Crucially, non-human primates appear to be limited in their ability to learn and represent the hierarchical structure of sequences. We consider the evolutionary implications of these differences and suggest that limitations in sequential learning may help explain why non-human primates lack human-like language.

Christopher M. Conway*
Morten H. Christiansen†
Dept of Psychology, Uris Hall, Cornell University, Ithaca, NY 14853-7601, USA.
*e-mail: cmc82@cornell.edu
†mhc27@cornell.edu

Sequential learning, by which we mean the ability to encode and represent the order of discrete elements occurring in a sequence, is a ubiquitous facet of cognition. Many of the events that we observe, as well as the behaviors we produce, are sequential in nature. From learning a particular behavioral sequence, such as a dance routine, to encoding meaning from a speech stream, sequential learning processes are at work. In humans, the ability to deal with complex sequential structure is perhaps most evident in language acquisition and processing (see Box 1). But sequential learning is not confined to humans. In order to adapt and survive, all higher organisms must learn to operate within a temporally bounded environment where sequential events occur.

To understand human sequential learning more fully, comparative studies of non-human primates are essential. After all, human cognition is merely one specific instance of primate cognition in general[1]. By exploring the abilities and the limitations that other primates have for processing sequential information, we can begin to understand the origins of such capabilities in humans as well as the unique aspects of human sequential processing.

Although there has been ample research aimed at investigating sequencing skills in non-human primates (for reviews, see Refs 2,3), few studies have provided direct comparisons with humans. The focus of this paper is to review data from research involving both non-human primates (hereafter, 'primates') as well as humans. We organize the data into three progressively more complex abilities: learning fixed sequences, encoding statistical regularities of sequences, and learning hierarchical structure.

Learning fixed sequences

Perhaps the simplest type of sequential learning has to do with the learning of an arbitrary, fixed sequence. In humans, this type of sequential learning corresponds to remembering a phone number or producing a stereotyped sequence of actions.

Learning action sequences by observation

A series of studies has examined learning in capuchin monkeys (*Cebus apella*), chimpanzees (*Pan troglodytes*), and human children (ages 2, 3, and 4 yrs) using a task designed to simulate natural sequential feeding behaviors[4–6]. These experiments used an 'artificial fruit' that functionally approximated food found in the wild. Subjects observed the experimenter bypassing one or more of the fruit's defenses using a particular arbitrary sequence of actions; afterwards, the subjects were allowed to manipulate the fruit in order to procure a treat contained within.

In general, when the artificial fruit consisted of only two sub-components, both non-human and human subjects copied the two-action, fixed sequence that they observed[4,6]. However, the human children copied the details of the actions more faithfully than did the primates (but see Box 2,

Box 1. Sequential learning and language

There is an obvious connection between sequential learning and language: both involve the extraction and further handling of elements occurring in temporal sequences. It is therefore not surprising that the use of sequential learning tasks has become an important experimental paradigm for studying language acquisition and processing[a].

Fixed sequences
The use of fixed sequences can be found at different levels in language. At the sentence level, idioms (e.g. '*letting the cat out of the bag*') and stock phrases (e.g. '*once upon a time*') are used as fixed word combinations. At the lexical level, words are fixed sequences of phonemes.

Statistical learning
Although words may be represented as fixed sequences, they are likely to be discovered originally via statistical learning. Eight-month-old infants appear to be capable of using transitional probabilities between syllables in a continuous sequence of auditory material to discover the component trisyllabic words of this nonsense language[b] (see Fig. 3 in main article). The importance of statistical learning in word segmentation is further underscored by the use of connectionist sequential learning networks to model both the infant data[c] and the process of speech segmentation more generally[d,e].

Hierarchical structure
Words in sentences are not merely strung together; rather, they are organized into phrases in a hierarchical manner. For example, the sentence '*The mouse chased the cat*' consists of two phrases: '*the mouse*' and '*chased the cat*', with the latter phrase containing a subphrase, '*the cat*'. Within phrases there is a predictable order of elements (e.g. the presence of the determiner, *the*, is a strong predictor of a following noun). Results from a sequential learning task have shown that both adults and children acquire more of the underlying structure of an artificial language when such predictive constraints are present[f]. The encoding of hierarchical linguistic structure in sequential learning devices has been further demonstrated in connectionist simulations of complex sentence processing[g,h].

Common neural basis of language and sequential learning?
Recent research suggests that language and sequential learning overlap not only in the processing of sequential structure, but also in neural mechanisms. Preliminary evidence has shown that agrammatic aphasics (typically with damage to Broca's area) who have severe problems with the hierarchical structure of sentences also have problems with sequential learning (M.H. Christiansen *et al.*, unpublished data). Furthermore, training aphasic patients on non-linguistic hierarchical processing results in improvements on complex linguistic constructions (P.F. Dominey *et al.*, unpublished data), indicating a causal link between sequential learning and language.

Recent neuroimaging studies with normal populations underline this link by showing that subjects trained on a sequential artificial language have the same event-related potential (ERP) brainwave patterns in response to ungrammatical sentences from this language as to ungrammatical natural language sentences (K. Steinhauer *et al.*, unpublished data). Moreover, incongruent musical sequences elicit ERP patterns that are statistically indistinguishable from syntactic incongruities in language[i]. Magnetoencephalography results suggest that Broca's area plays a crucial role in the processing of music sequences[j]. Together, these studies suggest that Broca's area might provide a common neural basis for learning and processing linguistic and non-linguistic sequential structure.

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caveat 1). In addition, when tested with a more complex fruit, chimpanzees were able to learn an arbitrary four-action, fixed sequence[5].

Serial ordering of visual stimuli: the role of planning
Another study compared Japanese monkeys (*Macaca fuscata*), a chimpanzee, and human adults in their learning of the serial order of visual stimuli[7]. Between two and four colored circles, each of a different size, appeared on a touch screen; subjects were required to press each stimulus in a pre-determined order (see Fig. 1a). Correct sequences were rewarded with an electronic chime and food treat; incorrect selections resulted in a 5 s blackout. The primates, but not the humans, received pre-training before testing (see Box 2, caveats 2,3).

Reaction times for each item in a list were collected for all trials. Across all species, 'monotonic' lists (e.g. going from the smallest circle to the largest) appeared to be easier to learn than non-monotonic lists (no logical order), as evidenced by shorter reaction times and a higher percentage of correct trials. More striking, however, was a comparison of reaction times on a condition in which list items

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Box 2. Caveats when comparing non-human and human performance

(1) *Imitating a non-conspecific*: Non-human primates are more likely to imitate the actions of a conspecific as opposed to those of a human[a]. In the experiments described in this article, the non-human primates might have been more successful in copying the action sequences if the model had been a conspecific instead of a human.

(2) *Training non-verbal animals* (i): Some studies incorporate extra training for non-human subjects. Although one can argue that this reflects a limitation in primate learning abilities, it is also true that because they are non-verbal animals, non-human primates will necessarily require training in the form of conditioning (but see also caveat 3).

(3) *Training non-verbal animals* (ii): Because non-human primates must usually be extensively trained before they can adequately perform a task, their performance might not reflect 'genuine' abilities[b].

(4) '*Upgraded' primates*: Some experiments use particular subjects who have had previous experience and training with numbers, symbols or simple language systems (e.g. the chimpanzee, Ai). In a sense, such subjects develop an 'upgraded mind'[c]. We must be cautious when drawing inferences based on these special cases.

(5) *Homology versus analogy*: Similar test performance in primates and humans does not necessarily mean that the underlying mechanism is the same for both species[d]. Instead of a homology (the same evolutionarily origins), the mechanism could be an analogy (operating under the principle of convergent evolution).

(6) *Methodological differences*: Performance differences between two species could reflect differences of experimental methodology or procedure, rather than actual differences in cognitive ability[b].

(7) *Natural context versus the laboratory*: There is a huge gulf between what an animal does in the wild and what it will do in a laboratory, depending heavily upon how the experiment is designed[b]. This can have one or more implications: a primate is likely to be more capable in its own natural context; alternatively, the laboratory setting could induce an ability the primate would not be likely to learn otherwise.

(8) *Human experience*: For many of the experimental tasks used, humans have had considerable previous experience with similar or related activities, whereas non-human primates often have not. Thus, humans might have an 'unfair' advantage in some experiments (e.g. list learning or hierarchical play behavior).

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appeared to be using a 'collective search' strategy, identifying all target items before actually selecting them (Fig. 1b). Finally, the chimpanzee subject seemed to be using serial searches on non-monotonic lists but collective searches on monotonic lists. These results might indicate differences in the manner that humans and primates encode and represent serial order. The collective search strategy, which presumably requires a form of 'planning', was used to a greater extent in humans, a lesser extent in chimpanzees, and not at all in monkeys.

Additional evidence further corroborates the suggestion that chimpanzees, like humans, use planning to help them perform serial order tasks[8]. A female chimpanzee ('Ai') with extensive experimental training using symbols and numerals[9] participated in a serial recognition task similar to that described above, but using numerals instead of colored circles. Ai was required to press three numerals on a screen in ascending order and was rewarded for doing so. To explore Ai's search strategy further, additional 'switch trials' were included: once Ai correctly selected the first numeral, the onscreen locations of the two remaining stimuli were immediately switched.

If Ai was using a collective strategy, we might expect switch trials to have a marked detrimental effect on her performance; however, if she was using a serial search strategy instead, presumably switch trials would not be as disruptive. The data suggested the former: on switch trials, her accuracy dropped from 94% to 45%. Furthermore, Ai's reaction times on the standard trials fit the general pattern (discussed above) of a collective search strategy. Additionally, Ai's hand movements were analyzed, showing that she often corrected the trajectory of her hand during a switch trial. The researchers concluded that not only was Ai planning the correct sequence before initiating her movements, but she was also monitoring her movements during execution. They believed that the presence of these processing stages (planning, executing and monitoring) point to the kind of cognitive processing demonstrated by humans (but see Box 2, caveats 4,5).

Representing sequences: encoding ordinal position
When humans and non-humans learn arbitrary lists of items, how are the sequences represented? One possibility is that subjects simply create associations between items in a sequence. Another possibility is that subjects learn the ordinal positions of items; that is, they associate each item with its position in the sequence. Encoding ordinality might be a more efficient mode of learning sequences compared with simply associating consecutive items in a sequence. Several studies have provided evidence that both macaque monkeys (*Macaca mulatta* and *Macaca fascicularis*) and chimpanzees learn the ordinal position of sequential items within a list[10–12].

In one study[10], rhesus monkeys first learned four-item lists consisting of colored photographs

disappeared after they were touched. On both monotonic and non-monotonic lists, monkeys' reaction times gradually decreased after each consecutive item. The author inferred that the monkeys were using a 'serial search' strategy; that is, they looked for the first item, selected it, then looked for the next item, selected it, and so on (see Fig. 1b). The human adults' reaction times, on the other hand, were longer for the first list item but then were consistently short for all remaining items. They
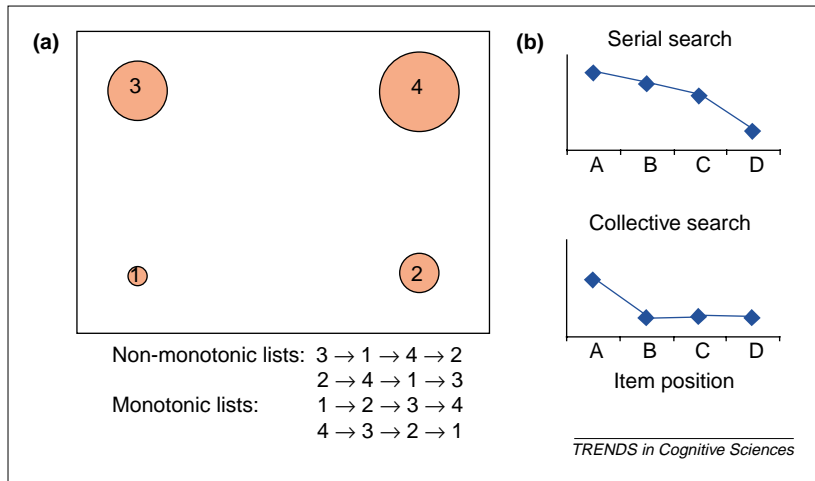
(a)

(b)

Fig. 1. Serial ordering of visual stimuli in Japanese monkeys, a chimpanzee, and human adults[7]. (a) Visual display showing experimental stimuli. Two, three or four circles of different sizes appeared in the corners of the screen simultaneously (locations were randomized and counterbalanced across trials). The color of the circles signaled whether a monotonic (e.g. $1 \rightarrow 2 \rightarrow 3 \rightarrow 4$) or a non-monotonic list (e.g. $3 \rightarrow 1 \rightarrow 4 \rightarrow 2$) was being tested. Subjects were trained by trial-and-error to press each item in the appropriate order. As each item was selected, it either disappeared or remained on the screen. (b) Serial versus collective search strategies. The existence of two general types of reaction time (RT) patterns indicates two different kinds of search strategies. In a serial search strategy, RTs decrease incrementally for each item in the list. In a collective search strategy, the RT for the first item is large but for the remaining items, RTs are smaller and roughly equal. Humans displayed the collective search strategy exclusively whereas the chimpanzee and monkey subjects used this strategy only partially or not at all. (The plots represent idealized trends from Ref. 7, not actual data.)

(see Fig. 2a,b). Next, they were tested on derived lists, which contained the same items as before but were grouped together in different combinations (see Fig. 2c). Some of the derived lists maintained the original ordinal positions while the positions on other lists were changed. When ordinal position was maintained, the monkeys learned the lists with few errors but when the positions were changed, the lists were as difficult to learn as novel lists. This is analogous to the performance exhibited by human adults on a similarly constructed task[13] and might point to similarities in the way humans and primates represent fixed sequences.

Summary

Primates appear to be capable of encoding, storing and recalling arbitrary fixed sequences consisting of motor actions[4–6] as well as visual stimuli[14,15]. For example, Ai is capable of remembering a sequence of up to five numbers, which is comparable to human preschoolers[16]. Furthermore, there is evidence that primates encode and represent a list of sequential items by learning each item's ordinal position[10–12] rather than associating successive items. However, primates might have at least one limitation in their ability to encode fixed sequences. Although humans, and to some extent chimpanzees, showed evidence of planning their movement sequences before executing them, monkeys did not do so[7]. However, list learning is only one facet of sequential learning. Next, we consider the capacity for encoding statistical information presented in sequences.

Statistical learning

Many sequential patterns are not fixed but rather consist of combinations of frequently co-occurring elements. For example, the sound sequences *funny* and *robot* each occur much more frequently in human speech than does the sequence *nyrob* (e.g. in the middle of the phrase *funny robot*). Being sensitive to such frequency information might enable new language learners to extract words from a continuous speech stream. In fact, previous research has demonstrated that 8-month-old infants are able to do this[17].

In a similar vein, many mammalian species are sensitive to statistical information in the environment[18] but previous studies have not directly compared non-human with human performance. However, a recent study[19] engaged cotton-top tamarins (*Saguinus oedipus*) in a statistical learning task similar to that used previously with human infants[17] (see Fig. 3). The monkeys first were exposed to a 20-minute sequential speech stream, consisting of four different trisyllabic nonsense words (e.g. *tupiro, golabu, bidaku, padoti*) concatenated together in random order. The boundaries between words were not marked by any acoustic or prosodic cues (Fig. 3a). Afterwards, the tamarins were exposed to different test sound sequences and were assessed on whether they oriented towards the sound when it was played. Some of the test sequences were words that were contained within the speech stream, some were non-words, which contained syllables in an order that had not occurred in the speech stream, and others were part-words, which contained syllable sequences spanning a word boundary (Fig. 3b). During the test, the tamarins were significantly more likely to orient towards non-words than to words, suggesting that they had discriminated test sequences on the basis of syllable order. The tamarins also were significantly more likely to orient towards part-words than to words, indicating that they were sensitive to the frequency of the syllable combinations. These results, which mirrored those of human infants (Fig. 3c), indicate that cotton-top tamarins – and presumably other primate species – are able to encode some of the statistical regularities present in language-like, auditory sequences. However, it is important to note that the tamarins were exposed to a 20-minute speech stream, whereas the human infants demonstrated statistical learning after only a 2-minute exposure.

More generally, this type of experimentation can provide a fruitful basis for the study of comparative cognition, and indeed, the same experimental paradigm has been used extensively to study complex sequential learning in pre-verbal infants[20]. That article dealt effectively with some common methodological difficulties (e.g. see Box 2, caveats 3,6,7) because it compared non-human subjects with pre-verbal infants using the same procedures for both species. Results from such research would be likely to contribute greatly to our understanding of non-humans' sequential learning
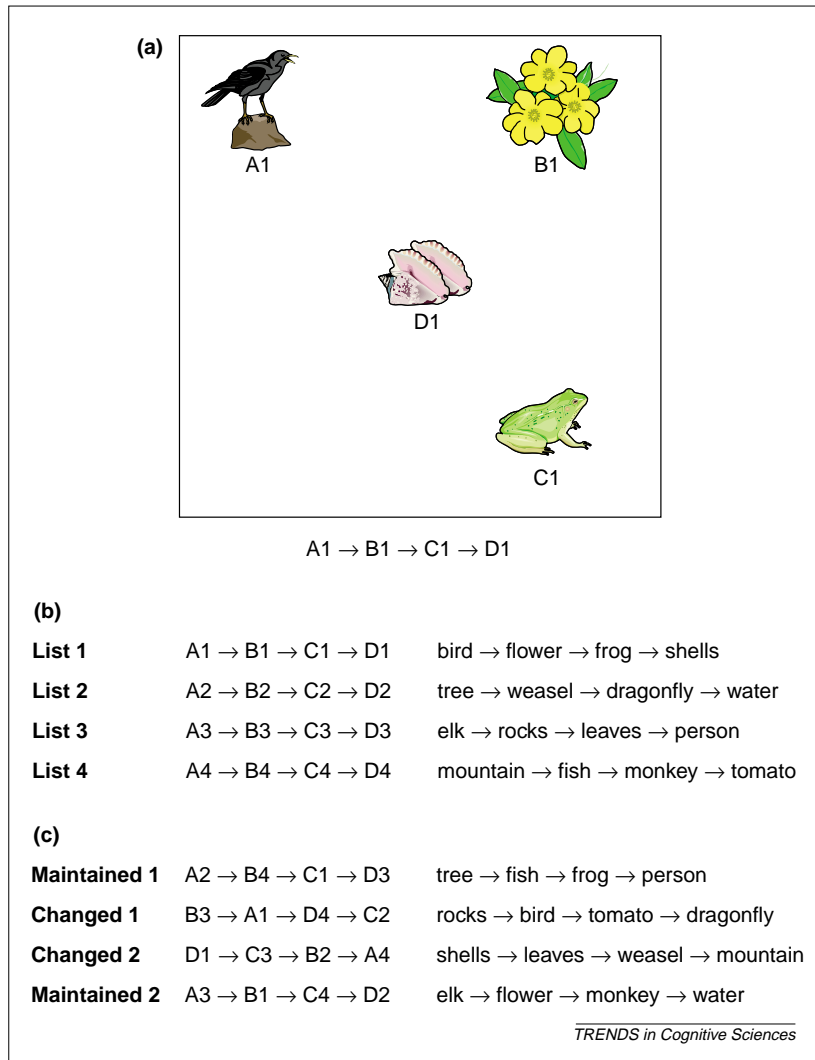
Fig. 2. Representation of ordinal position in rhesus monkeys[10]. (a) Monkeys were presented with up to four colored pictures (in randomized spatial configurations) on a touch-screen monitor and were trained to press each one in a particular order. Shown is one possible spatial configuration for List 1. (b) Original lists: sixteen pictures were grouped into four lists. An alphanumeric symbol signifies each item's ordinal position on the original list: the letter refers to the item's position (A is first, B is second, etc.) and the number refers to the list on which it appeared. (c) Derived lists: once a 75% accuracy level was obtained with the original lists, subjects were presented with four new lists to learn, which contained the same pictures in new combinations. On some lists ('maintained lists'), the items were in the same ordinal positions as the original lists, whereas on others ('changed lists'), the items were in new positions. Subjects were trained on each list until they reached criterion (75%) performance. Maintained lists were much easier for the subjects to learn than changed lists, suggesting that the monkeys had learned the original lists in terms of each item's ordinal position.

capabilities, and would provide a clearer evolutionary perspective on human statistical learning.

Despite the tamarins' human-like performance in statistical learning, there may be other aspects of sequential learning that non-humans lack. For instance, human language also involves relationships between elements that are not directly adjacent to one another in the speech stream. We therefore consider the third, most complex form of sequential learning: the acquisition of hierarchical structure.

Hierarchical organization of behavior
In the study previously described, the tamarin monkeys segmented the artificial speech stream by using statistical information pertaining to consecutive elements (pair-wise associations). In more complex learning domains, this type of sequential learning alone might not be sufficient. Instead, it might be necessary to encode the frequency information for more than just the previous element of a sequence – perhaps the previous two or more elements. For example, in the repeating sequence '1, 3, 2, 3, 1, 2' each item can be followed by one of two possible items (e.g. '1' is followed by either '3' or '2'). Only by taking into account the context in which an item occurs can one accurately predict the subsequent item[21] (e.g. knowing that '1' is preceded by '2' allows one accurately to predict '3'). In such situations, it can be useful to 'chunk' groups of items together[22]. Such a strategy might provide the basis for hierarchical processing, in which primitive units are combined to create more complex units, which in turn can be combined to create even more complex units, and so on.

Hierarchical structuring of sequences is essential for such complex tasks as language processing and problem-solving[23]; it also allows efficient organization of motor acts[24,25], including tool-use[26] and throwing[27]. Unfortunately, it is difficult to know to what extent primates exhibit hierarchical processing because often this can only be inferred from patterns of reaction times or errors. Although reaction times suggest that monkeys use a chunking strategy to aid recall of a sequence[28], this might not necessarily implicate hierarchical organization. Instead of using such an inferential technique, one possible solution is to look for signs of hierarchical organization in their produced behaviors.

Hierarchical learning: a case study
Researchers have described a group of African mountain gorillas (*Gorilla g. beringei*) that observationally learn sequences of complex manual actions used to bypass the natural defenses of edible plants[29]. The gorillas appear to organize the sequences into a hierarchical structure, as each goal (e.g. remove the indigestible material from the plant) is composed of sub-goals (e.g. remove the spines), which in turn might consist of sub-processes. However, from this data it is not clear how such behavior compares with human behavior; the researchers suggest that the hierarchical complexity (number of embedded layers) displayed by the gorillas may be relatively limited.

Spontaneous manipulations
Another program of research investigated the spontaneous behavior of common chimpanzees, a bonobo (*Pan paniscus*), and human children (between 6 and 24 months)[30–32]. Subjects were presented with a set of six objects (e.g. cups, rings and sticks that were blue, red or yellow) in various combinations. They were allowed to manipulate the objects freely for about 5 mins – without any reinforcement – and their actions were coded in terms of the order of the acts, relations between the acts, and the objects involved in the acts.
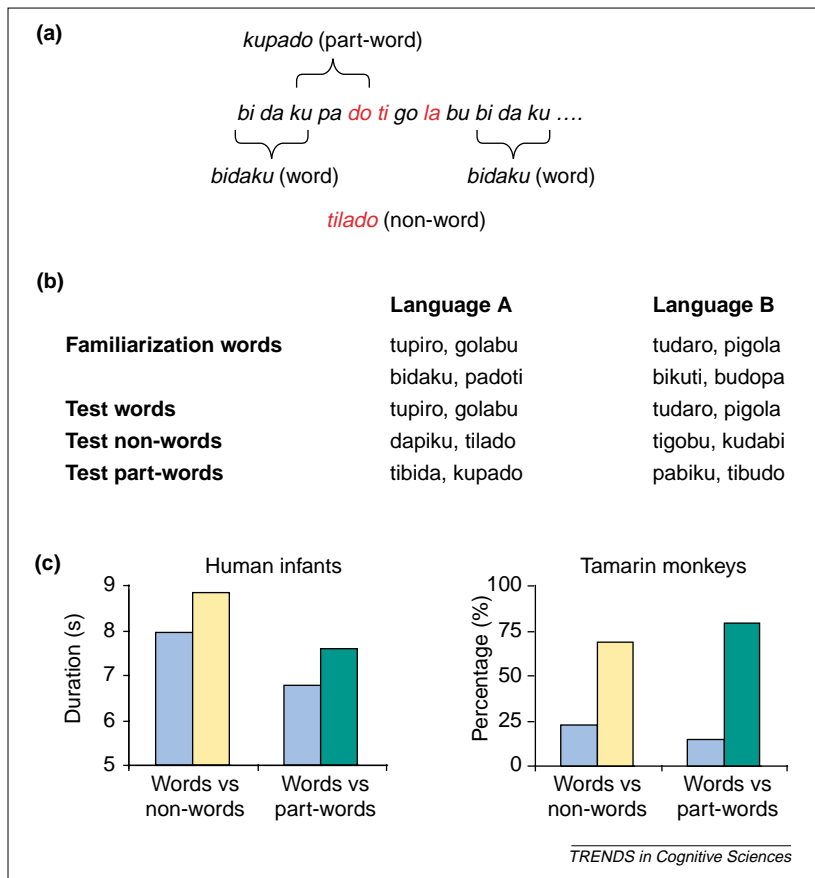
(a)

kupado (part-word)

bi da ku pa do ti go la bu bi da ku ….

bidaku (word)   *bidaku* (word)

tilado (non-word)

(b)

	Language A	Language B
Familiarization words	tupiro, golabu	tudaro, pigola
	bidaku, padoti	bikuti, budopa
Test words	tupiro, golabu	tudaro, pigola
Test non-words	dapiku, tilado	tigobu, kudabi
Test part-words	tibida, kupado	pabiku, tibudo

(c)

Human infants — Tamarin monkeys

Fig. 3. Statistical learning in human infants and tamarin monkeys[17,19]. (a) Subjects were exposed to a continuous auditory stream of syllables consisting of a random ordering of nonsense 'words' (e.g. *bidaku*). No acoustic cues marked word boundaries. After exposure to the speech stream, subjects then were exposed to several test stimuli. Words (e.g. *golabu*) consisted of three consecutive syllables that always occurred together in the speech stream; non-words (e.g. *tilado*) consisted of syllables that were found in the speech stream but had not occurred together; part-words (e.g. *kupado*) consisted of the last syllable of one word combined with the first two syllables of another word. The dependent variable in the infant study was the amount of time the infant oriented to the test stimulus (using the familiarization-preference procedure[46]), whereas for the tamarin study it was the presence or absence of an orienting response (whether the monkey turned towards the speaker when the stimulus was played). (b) The stimuli used in both language conditions of the tamarin study are shown. (The stimuli used in the human infant study are very similar, although not identical, to those listed here.) (c) Comparison of human infant and tamarin data. The infants oriented significantly longer to both non-words (yellow bars) and part-words (green) than they did to words (blue). Likewise, the tamarins were significantly more likely to orient towards non-words and part-words rather than to words.

For example, a 'routine' was scored if a subject combined acts on objects into a coordinated sequence of mappings (e.g. one hand picks up and holds one object; the other hand uprights a second object; then the first object is used to knock over the second object). In addition, a routine was considered to have hierarchical organization if two separate elementary routines were integrated together into a complex whole.

The results revealed that the primates performed fewer of their acts in parallel (i.e. performing two acts simultaneously) than 2-year-old children. Importantly, only 8% of the primates' sequence routines showed hierarchical complexity, far less than that displayed by human children.

Seriation strategies
A third approach investigated combinatorial strategies in capuchin monkeys, chimpanzees,

bonobos and human children[33,34]. Nesting cups were used, each varying in size so that the smallest could fit into one that was slightly larger, which in turn could fit into the next largest, and so on (i.e. cups could be 'nested' or seriated). The experimenter demonstrated nesting the cups using a hierarchical strategy (or 'subassembly'; see Fig. 4a). Afterwards, the experimenter took the cups apart and placed them in front of the subjects, who were verbally encouraged to combine the cups (the primates also received food treats in between trials, regardless of performance). The subjects' behavior in combining the cups was coded in terms of three possible strategies: 'pairing', 'pot' and 'subassembly' strategies (Fig. 4a).

The human children, tested between the ages of 11 and 36 months, displayed a developmental progression of strategies[34] (see Fig. 4b). At the youngest ages, children most frequently used the pairing strategy, although by 16 months, the pot strategy was most frequent. At 20 months and older, children also began to incorporate the most hierarchically complex strategy, subassembly. Interestingly, the development of these strategies in children has (controversially) been argued to parallel the development of phonological and grammatical constructions present in language[26]. These results differ strikingly from those of the primates[33]. Capuchin monkeys initially were severely limited at this task and only after undergoing an additional training procedure – which encouraged them to manipulate the cups – did they display combinatorial activity at all (note that the apes had already had previous experience with manipulating objects in experimental settings, whereas the monkeys had not). Although all three species eventually became proficient at nesting the cups, they never used the subassembly strategy as their dominant method – even though this was the strategy demonstrated by the experimenter – relying instead on the pairing and pot strategies (Fig. 4b).

Summary
There appear to be limitations on primates' abilities to learn the hierarchical structure of manual actions. Although there is evidence that gorillas hierarchically organize their actions for food preparation tasks[29], we have also seen that apes and monkeys rarely use hierarchical routines in their spontaneous[31] and learned[33] actions. However, it is not entirely clear whether these limitations reflect a genuine cognitive limitation or are merely a result of methodological or contextual discrepancies (Box 2, caveats 6,7). Furthermore, these species differences might be a result of human children having previous experience with hierarchical behaviors, rather than innate species differences (Box 2, caveat 8). Finally, it should be noted that these three studies tested whether the subjects would *spontaneously* engage in certain hierarchical behaviors, not whether they were *capable* of performing these behaviors. It is certainly possible that non-human primates have a
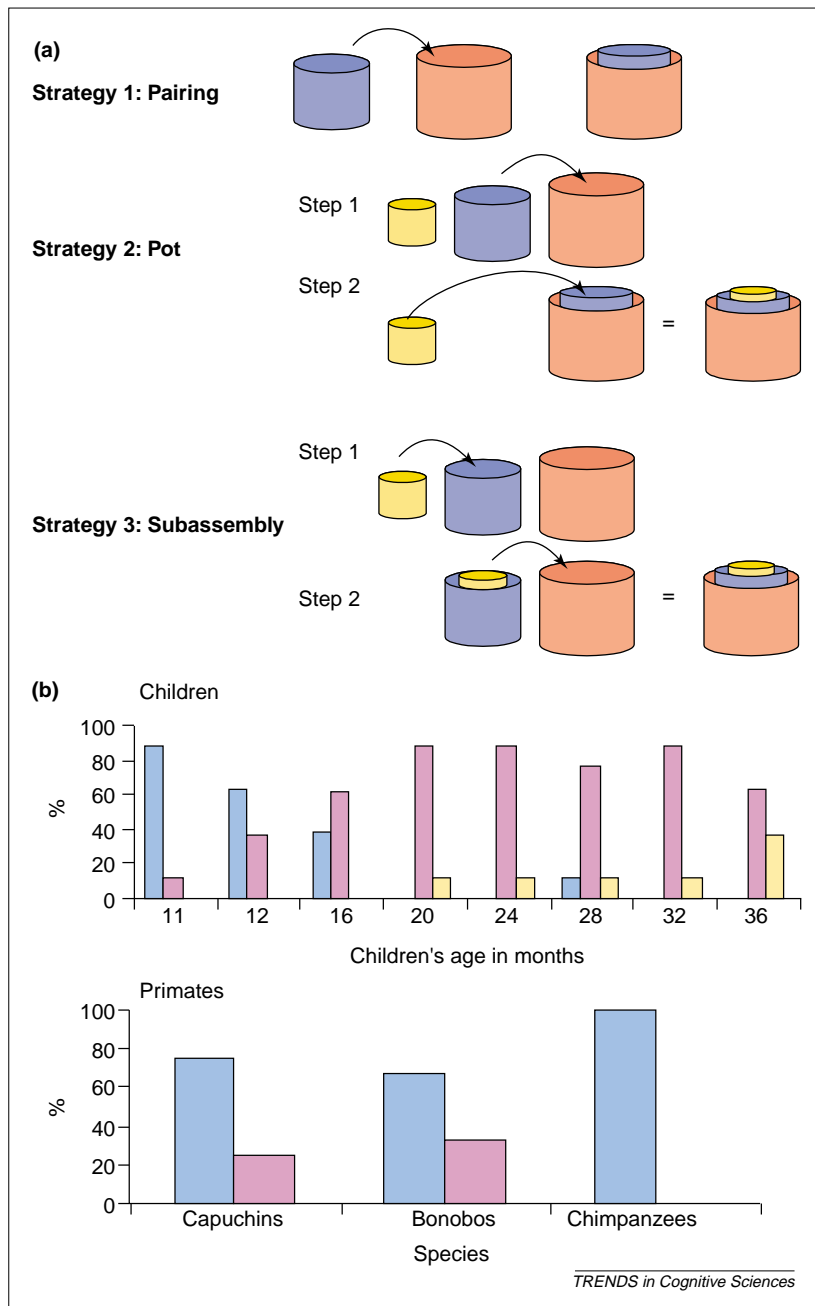
Fig. 4. Combinatorial strategies used by human infants[34], chimpanzees, bonobos, and capuchins[33]. (a) Three possible strategies for combining nesting cups were identified. The pairing strategy is the simplest method, consisting of merely stacking or nesting two cups. In the 'pot' strategy, cups are placed one at a time into another cup. The most complex strategy, 'subassembly', requires hierarchical organization: two or more cups are combined to form a single unit, which is then placed into another cup. (Note that the coloring of the figures is not representative of the actual experimental objects). (b) The percentage of human infants and primates that used a particular dominant strategy. A strategy was considered dominant for a particular subject if that subject used the strategy more often than any other. Children initially used the pairing strategy (blue bars), then the pot strategy (magenta), and eventually incorporated subassembly (yellow) into their routines. Primates, on the other hand, never used subassembly as their dominant strategy, instead relying upon the pairing and pot methods. The lack of the subassembly strategy in primates might reflect a cognitive limitation in comparison to humans. (Adapted from Refs 33,34).

hierarchical learning capacity to which the experimental tasks were not sensitive.

Conclusion

The studies we have reviewed indicate that there is considerable overlap between the performance of

humans and non-humans on a variety of sequential learning tasks. For instance, both humans and non-humans appear to encode fixed sequences by ordinality, can discover coherent units ('words') in a continuous speech stream using statistical learning, and are capable of some level of hierarchical organization of behavior. However, there are also important limitations on primate sequential learning, in particular on the more complex hierarchical learning tasks. More generally, there is some evidence of a phylogenetic trend in primate cognition (noted elsewhere[35]), with humans performing better than apes, and apes performing better than monkeys.

The pattern of performance differences across species might suggest that human sequential learning derives from evolutionarily old cognitive substrates, from which the sequential learning abilities of extant primates also have evolved. Of course, similarity of performance does not necessarily entail homologous mechanisms[36] (Box 2, caveat 5). However, evidence from neurobiology appears to substantiate the notion of a homologous substrate for sequential learning in humans and primates. Studies of humans[37,38] and primates[39,40] indicate that premotor and prefrontal cortices are involved in sequential learning. Furthermore, studies in which both humans and Japanese monkeys were engaged in the same task have demonstrated that the learning of novel fixed sequences in both species involves the anterior portion of the supplementary motor area[41,42]. Thus, current evidence suggests that the learning of fixed sequences is homologous in primates and humans. We expect that further homologies eventually will be found for statistical and hierarchical learning.

Despite these potential homologies, it is also clear that humans outperform non-humans on more complex sequential learning tasks – in particular the learning and processing of hierarchically organized temporal sequences. We speculate that this species-specific difference is an important piece of the language evolution puzzle. Language fundamentally involves hierarchical structure (see Box 1) as the basis for unbounded productivity, which is one of the hallmarks of human communication. The limitations on primate hierarchical learning might thus be one of the key reasons that they have not developed advanced language abilities.

Supporting evidence is expected to emerge from studies looking more closely at primates' abilities for hierarchical learning. Further studies will need to uncover the species-specific differences in the ability to chunk elements together into units that can then be further combined with other elements in a hierarchical manner. We expect these studies to uncover differences between humans and non-humans that are important for the acquisition of linguistic structure[43]. Of course, there are likely to be additional reasons why non-human primates are incapable of human-like language, such as an inability to integrate multiple sources of information[44,45]. We anticipate that future studies will clarify the relationship between sequential learning and language as well as provide further insights into the evolution of sequential learning, language, and cognition.

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