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Sequential recall of meaningful and arbitrary sequences by orangutans and human children: Does content matter?

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Abstract Do visual cues such as size, color, and number facilitate sequential recall in orangutans and human children? In Experiment 1, children and adult orangutans solved two types of sequences, arbitrary (unrelated pictures) and meaningful (pictures varied along a spectrum according to the size, color, or number of items shown), in a touchscreen paradigm. It was found that visual cues did not increase the percentage of correct responses for either children or orangutans. In order to demonstrate that the failure to spontaneously seriate along these dimensions was not due to a general inability to perceive the dimensions nor to an inability to seriate items, in Experiment 2, orangutans were trained on one type of sequence and tested on novel sequences organized according to the same rule (i.e., pictures varied on the number spectrum only). The orangutans performed significantly better on novel meaningful sequences in this task than on novel arbitrary sequences. These results indicate that, while orangutans and human children share the ability to learn how to order items according to their size, color, or number, both orangutans and humans lack a cognitive propensity to spontaneously (i.e., without prior training or enculturation) order multiple items by size, color, or number.

Keywords Sequential learning · Great apes · Children · Development · Memory · Monotonicity

Introduction

Sequential learning is critical for solving complex problems. Consider how some primate species process certain types of foods. Whether dipping for ants with a stick, cracking a nut, or hunting a small animal, in each case, a series of steps is required to obtain the nutrition available. Sequential behavior is also important for humans in a cultural context, when using language and engaging in ritual behaviors (Hulse 2002, p. 5). In addition to being useful in problem-solving, sequence learning tasks have been utilized to study a variety of cognitive phenomena such as working memory in chimpanzees (Inoue and Matsuzawa 2007) and humans (Corsi 1972), numerosity (Brannon et al. 2006), event recall (Bauer and Mandler 1989), and maze-solving (Hull 1952, chap. 6).

In fact, many animal species, from rats to pigeons to primates, are able to learn "lists," that is, to perform a sequence of actions or select target items in a particular order (Swartz et al. 1991; Terrace 2001). Research with sequential tasks implemented on touch-sensitive screens has shown that rhesus monkeys can learn a sequence of items (e.g., four distinct pictures) when given incremental training starting with the first item in the list (Swartz et al. 1991) or when given progressively complex trial-and-error learning conditions (Swartz et al. 2000). Animals can also develop knowledge of the ordinal positions of specific items in a sequence (D'Amato and Colombo 1988; Harris

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et al. 2007; Pfuhl and Biegler 2012; Scarf and Colombo 2011). Crucially, relating items (i.e., images) in a sequence does not require verbal ability, as shown by the mastery of sequential lists by pigeons and monkeys (Swartz et al. 1991) and improvements in performance with greater expertise (Terrace et al. 2003). Here we explore whether sequencing items based on visual—content—cues is a spontaneous behavior or one that must be explicitly trained and learned.

To study sequential behavior, Terrace and colleagues developed a widely used paradigm known as the simultaneous chaining paradigm, in which individuals must master an item-based rule (henceforth, "cognitive task"). In it, *n* pictures appear simultaneously on a touch-sensitive screen and must be touched in a specific sequential order before a reward is delivered. The different pictures (e.g., A → B → C) appear in different spatial arrangements from trial to trial (Terrace 2002; Fig. 1). This design requires that participants focus on the content of the pictures when responding with the correct sequence; attention to the spatial position of a picture offers no clue as to the ordinal position of that picture in the sequence. The cognitive task has been used in numerous experiments with pigeons, monkeys, apes, and humans (Ohshiba 1997; Subiaul et al. 2004, 2007; Swartz et al. 1991, 2000; Terrace 1991, 2005; Terrace et al. 2003). Previous research into serial memory has generally used arbitrarily related items that are not inherently ordered by visual cues like size, for example (Guyla and Colombo 2004; Harris et al. 2007; Subiaul et al. 2004).

The effects of certain visual cues in stimuli (such as size, color, and number) on spontaneous performance in sequence learning tasks have not been well studied in primates or young children. The ability to discriminate between larger and smaller quantities based on either number or size may be adaptive (e.g., when detecting food quantity or the number of aggressive conspecifics in the vicinity; Anderson et al. 2007; Bonanni et al. 2011; Shettleworth 2010, chap. 10) and is clearly evident in the behavior of many different animal species (Agrillo and Bisazza 2014; Anderson and Cordes 2013; Davis and Pérusse 1988). In captive tests, multiple species (including primates, felids, bears, birds, and fish) can spontaneously discriminate between two arrays with different numbers of food items or social companions (for a review, see Agrillo and Bisazza 2014). In humans, even 6-month-old infants can distinguish between visual arrays of different numbers of dots (Xu and Spelke 2000). And children as young as 2 years of age successfully pick out an array that contains the larger number of boxes (Brannon and Van de Walle 2001).

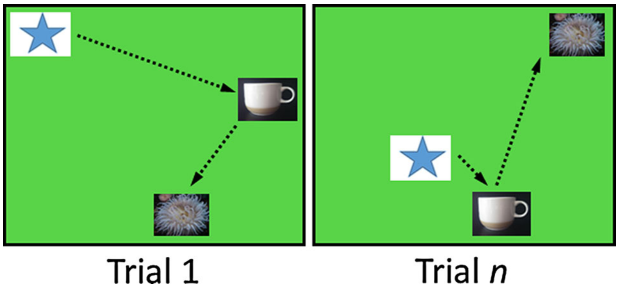


Fig. 1 Example of a three-item cognitive task sequence. Images must be selected in a certain order (here, star → mug → anemone). In Trial 1, figures appear in a random spatial configuration. On subsequent trials, the same images appear in different spatial configurations. *Arrows* are not shown during testing; they are included here for illustrative purposes only

Previous studies therefore show that, overall, very young children and some non-human animals are able to distinguish between two items or sets of items based on size or quantity. While there is some evidence that many species can implicitly seriate food items based on preference (Maslow 1933; Remis 2007), it is less clear how children and non-human animals spontaneously seriate multiple non-food items that vary on a particular visual dimension. Situations in which serial organization of this type may be useful include processing social dominance hierarchies (Paz-y-Miño et al. 2004) or spatially navigating between various fruiting trees based on the projected amount of food available at each tree. Alternatively, the ability to serially organize multiple items by size, number, or color may be uniquely constrained in humans by language. That is, the features of language—a rule-governed, serially organized system of conventionalized signs (Pinker 1991, 1994, chap. 4)—itself might uniquely constrain how humans think about and organize linguistic and non-linguistic items alike, driving us to impose serial order on all sorts of things based on observable cues.

Here, we explore whether certain features of stimuli can improve an individual's serial memory without explicit training. That is, do non-human great apes (*Pongo pygmaeus* × *abelii*) and preschool-age human children (*Homo sapiens*) spontaneously attend to and use visual cues of size, color, and number which predict the order of items in a multiple-item sequence? Although non-human great apes are the species most closely related to humans, they do not naturally use language to communicate. These orangutans (*P. pygmaeus* × *abelii*) were chosen to participate in this study because of their experience interacting with a touchscreen and prior training in seriating unrelated items (arbitrary sequences in the task described below).

In order for the task to be suitable for both humans and non-human apes, we selected cues that are not inherently verbal. Although it is possible that children may encode some features of the task verbally, Conrad (1971) found that children under the age of 5 years generally do not use covert speech to remember the names of items in a serial order task. The cues used here cause the appearances of the items to vary in predictable ways on scales of size, color, and number.

Previous research suggests that 9-month-old infants look longer at a reversal (e.g., smallest to largest) of a three-item monotonic sequence ordered by size than at a sequence going in the habituated direction (e.g., largest to smallest) (Brannon 2002). In addition, multiple-item sequences seriated by size monotonically (that is, ones that progress from smaller to larger items or from larger to smaller) are easier for 5- and 7-year-old children to learn than non-monotonic sequences, as gauged by the number of errors made in learning sequences (Terrace and McGonigle 1994). In experiments with three monkeys and one chimpanzee, Ohshiba (1997) found that the primates performed significantly better (as judged by the percentage of correct responses) on a four-item monotonic sequence organized by size than a non-monotonic sequence on at least one type of task. In addition, Brannon and Terrace (2000) attempted to train one macaque monkey on a non-monotonic numeric sequence but were not able to do so after a large number of training sessions; they subsequently trained the same monkey successfully on a monotonic (ascending) pattern. Therefore, the cues used in this research were chosen to vary monotonically along their particular dimension.

In order to test spontaneous responses to stimuli that varied monotonically on different spectra, we utilized two different types of sequence within the cognitive task. So-called “arbitrary” sequences consisted of three pictures that did not bear a relationship to each other: for example, star → mug → anemone (Fig. 2a). So-called “meaningful” sequences consisted of three pictures that were joined by a relationship in one of three categories: size (e.g., small to large, Fig. 2b), color (light to dark, Fig. 2c), or number (few to many, Fig. 2d). There is no reason to believe that great apes would have difficulty perceiving differences along these dimensions. As catarrhine primates, orangutans have trichromatic color vision (Jacobs and Williams 2000). Additionally, many animal species, including non-human primates, have been shown to use a so-called “approximate number system” to evaluate quantities (Cantlon and Brannon 2007; Cantlon et al. 2009).

A difficulty inherent in research on concepts of number is that there is a relationship between the number of identically sized items and the overall surface area of items in an image or array. We were interested in whether individuals would use any cue (whether number or surface area) to improve their performance; to make the task as transparent as possible, we used similarly sized items in sequences that varied on the “number” dimension.

If children or orangutans who have been trained to order arbitrary sequences use the visible content cues in the meaningful sequences to enhance memory for sequential lists, they will spontaneously exhibit improved recall on meaningful sequences compared to the arbitrary sequences. This may indicate that sequencing items according to visual features of size, color, and number accesses a natural cognitive tendency to sequence items by visible features. Alternatively, if there is no advantage to learning a meaningful sequence in comparison with an arbitrary sequence, one might conclude that such cues in a sequential learning paradigm are not used spontaneously and, instead, must be learned, much like ordering an arbitrary sequence of pictures is learned.

Experiment 1: spontaneous responses to tasks

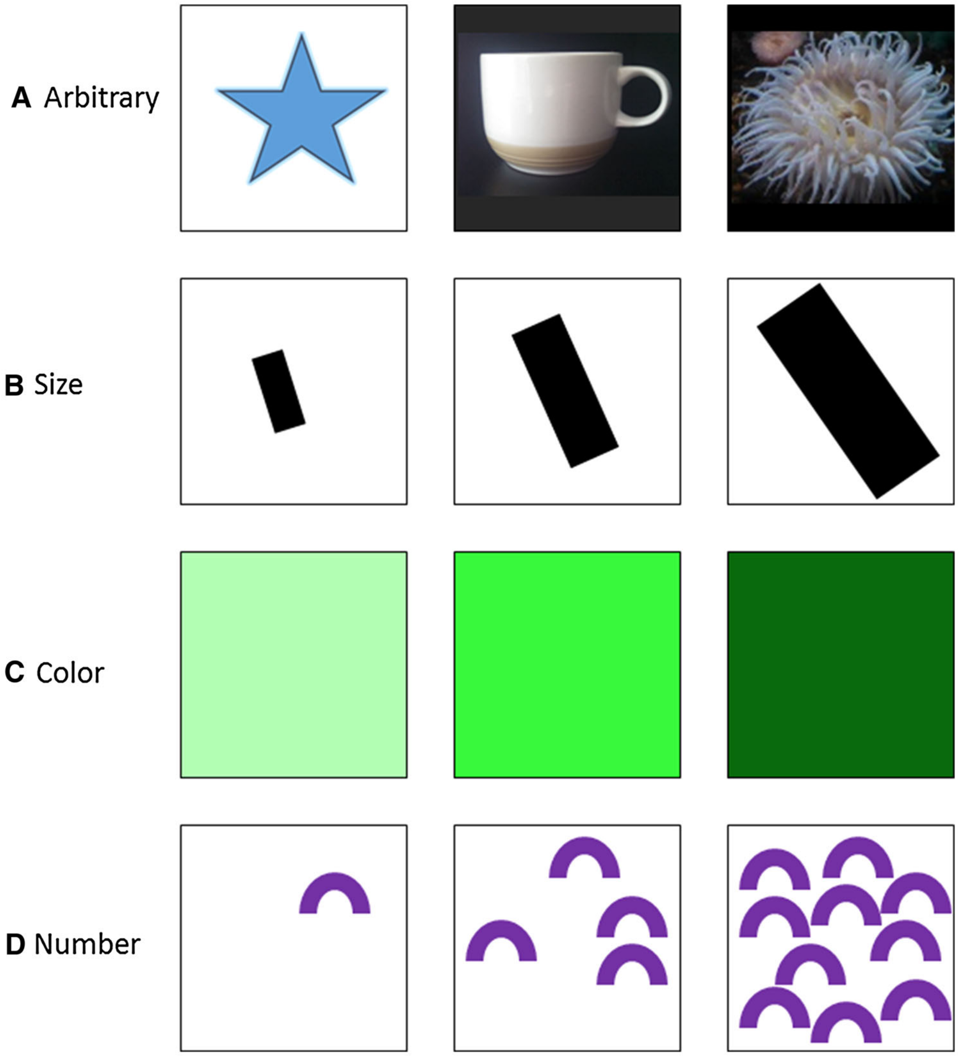
Methods and materials

Task

The purpose of Experiment 1 was to examine whether young children and orangutans spontaneously use content cues to learn and remember sequences in a simultaneous chaining paradigm or cognitive task (Terrace 2005). In this task, three different images (A, B, and C) appear simultaneously on a touchscreen. From trial to trial, the pictures change spatial position; this prevents individuals from using spatial cues to guide their responses. Subjects' task was to respond to each picture in a specific order, A → B → C (Fig. 1). In this study, the same three images were used for all trials in a single testing block. Subjects were required, by trial and error, to determine the correct order of the items. Visual and auditory feedback was given after correct and incorrect responses, as follows. When correct selection of a single item was made, a black border appeared around the image and the computer emitted a “ding” as auditory feedback. When three correct selections were made (for a correctly completed full sequence), a reward was given. When incorrect selection of a single item was made, the trial ended: The computer made a whooshing sound, and the screen went blank for a 2-s time-out. With any three-item list, the probability of a subject guessing the correct sequence on the first trial is $1/3 \times 1/2 \times 1/1 = 0.1667$, or 16.7 %.

Two sequence types were used: (1) In arbitrary sequences, the contents of the pictures were unrelated; (2) in meaningful sequences, the contents of the pictures varied predictably in size, color, or number. For example, a sequence of three images might vary by the size of a single object (small → medium → large: Fig. 2b), the color of the field (light → medium → dark: Fig. 2c), or the number of objects shown (1 → 4 → 12: Fig. 2d). For the picture items on the number scale, items could be either identical

Fig. 2 Examples of the sequence types. **a** Arbitrary sequence, **b** meaningful size sequence (from *left* to *right*, the single object in the images is initially small and grows larger), **c** meaningful color sequence (from *left* to *right*, the shade of the entire panel is initially light and grows darker), and **d** meaningful number sequence (from *left* to *right*, there are initially few objects in the image, and then many) (color figure online)



or nonidentical. The smallest number of items in the "number" sequences ranged from 1 to 5, the middle ranged from 2 to 10, and the largest ranged from 3 to 29. Both ascending (from few to many, small to large, and light to dark) and descending (from many to few, large to small, and dark to light) lists were used for the meaningful sequences.

Training protocols for children and orangutans differed due to the tendency in previous research for children to understand the task fairly quickly and for non-human primates to require more training before reaching criterion (see, e.g., Subiaul et al. 2007).

Orangutans

Participants Three adult orangutans, all housed at the Smithsonian National Zoological Park in Washington, DC, participated in this study: two adult females (Bonnie and Lucy) and one adult male (Kiko). All three were *P. pygmaeus* × *Pongo abelii* hybrids. These individuals had previously participated in sequencing studies involving arbitrary sequences on a touchscreen. They had also participated in other touchscreen and object-based tasks, but not other seriation tasks. This study was approved by the George Washington University (GWU) and Smithsonian Institution Institutional Animal Care and Use Committees (IACUC). Water was available ad libitum throughout the sessions, and individuals were not food-deprived before testing.

Apparatus All training and testing tasks were carried out with a MacBook (Apple, Cupertino, CA) laptop computer with a display screen (Dell, Round Rock, TX) and a MagicTouch (Keytec, Garland, TX) touchscreen attached. These were affixed to a mobile cart used to test orangutans in their various living enclosures. The cart was placed flush

Table 1 Orangutan participant training details for Experiment 1

Orangutan name	Sex	Age (years)	No. of training sessions	Highest accuracy (%)
Bonnie	F	35	142	93
Kiko	M	24	169	65
Lucy	F	38	288	87

with the enclosure edge so that the orangutan could touch the screen; a tube was used to dispense food rewards after correct responses.

Procedure

1. *Training* Orangutans received multiple training sessions on the cognitive task, details of which are presented in Table 1. Each training session consisted of 60 trials; a novel arbitrary sequence was used for each session. All orangutans met the criterion of achieving 65 % accuracy on a three-item sequence before beginning the experimental phase; this criterion was based on that used previously by Terrace et al. (2003). Chance performance level on a three-item list is 16.7 %; thus, the criterion was set to be nearly four times greater than chance performance.
2. *Testing* Once orangutans met criterion in the training phase, they began the experimental phase. One session comprised a block of 30 trials of an arbitrary sequence and a block of 30 trials of a meaningful sequence, for a total of 60 trials. The order of arbitrary and meaningful blocks was counterbalanced across sessions. Due to National Zoo restrictions on the apes' diets, the absolute number of trials given to orangutans did not exceed 60 trials in a session. Given the reduced number of trials per block in the testing phase, we cannot exclude the possibility that performance might have improved with a larger number of trials. Each orangutan completed a total of 30 sessions (10 sessions each with size, color, and number sequences; half of the sequences of each type were ascending, and half were descending); in each session, novel sequences were used. The variability of meaningful stimulus sets was essential to avoid inadvertently training apes during the experimental phase on one type of sequence (ascending/descending, size/color/number).

The duration of a single session was between 5 and 15 min. Testing occurred at various times between 7 a.m. and 3 p.m. Rewards for correct sequences consisted of a grape or other desirable food item and the "Jumping Man" video, a 5-s video of a man doing a backward flip accompanied by an audio track of either applause or a "yahoo."

Children

Participants Forty-eight typically developing 3-year-old ($N = 26$, $M_{\text{months}} = 41.3$, SD = 3.5, female = 15) and 4-year-old ($N = 22$, $M_{\text{months}} = 53.7$, SD = 3.0, female = 10) children were recruited at the National Museum of Natural History in Washington, DC. Children in this age group have been found in previous studies to be able to sequence arbitrary items in touchscreen tasks (Subiaul et al. 2007, 2012). In addition, this age group has not yet begun formal schooling and therefore would be unlikely to have learned seriation in an educational setting. According to parent-reported ethnicities, the children were 73 % white ($N = 35$), 4 % black ($N = 2$), 8 % Asian ($N = 4$), 2 % Hispanic ($N = 1$), and 12.5 % mixed race or other ($N = 8$). The parents of all children signed a consent form approved by the GWU Institutional Review Board. Children were asked for their assent before participating and did not participate if assent was not given. Data from three additional children could not be used due to experimenter error; data from two children were discarded due to interference from parents or other children; and three children did not complete the task due to low motivation. One additional child did not assent to taking part in the study.

Apparatus All tasks were carried out with an iMac (Apple, Cupertino, CA) computer with a MagicTouch (Keytec, Garland, TX) touchscreen attached.

Procedure

1. *Training* Before beginning their first task, children were trained on the cognitive task with a training set of arbitrary picture items. Because the basic format of the presentation of arbitrary and meaningful sequences was the same, children were trained only once, before they began the first task. A child was shown a practice sequence on the touchscreen; the experimenter prompted "Which of these do you think is picture number 1?" The child was allowed to touch various picture items, until they discovered the correct sequence of three items by trial and error. The reward after a correct sequence was verbal praise from the experimenter and the "Jumping Man" video.

2. *Testing* After children completed training, they began the experimental phase. Children were told that they would receive a sticker each time they "found jumping man" (selected the complete sequence correctly) and that at the end of the experiment, if they did well, they could get a larger sticker or toy. Children completed 10 trials of one type of sequence (arbitrary or meaningful); once they were finished, they completed 10 trials of the other type of sequence. The order of the sequence types (arbitrary and meaningful) was counterbalanced. Each child received only one type of meaningful sequence, for a between-subjects manipulation of this factor. A small sticker was placed on a "prize sheet" for each completed correct response (A → B→ C), and children were allowed to select a large sticker at the end of each task (e.g., after 10 trials). At the end of the session, children were allowed to choose a small toy. Total testing time was 10–20 min.

Statistical analysis Statistical analyses were carried out in SPSS 19 (IBM; Armonk, NY). Performance on each type of sequence in a session was calculated for each individual as the percentage of correct responses. For the individual orangutans, means from the arbitrary and meaningful sequences were compared to chance performance by single-sample *t* test and to each other by paired *t* test. Performance on ascending and descending sequences was also compared by *t* test. The effects of the subtype of meaningful sequence (size, color, and number), item density, and individual were evaluated by a mixed repeated-measures ANOVA. Because data were not normally distributed, Spearman's rank-order correlations were used to evaluate session number and percentage correct, to determine whether orangutans' performance improved with more experience in the paradigm. Finally, paired *t* tests were used to determine whether orangutans' scores were better in either the first or the second half of a testing block.

For children, because data were not normally distributed, Spearman's rank-order correlations with child age in months and performance on each type of sequences (arbitrary and meaningful) were used to determine whether scores were correlated with age. Performance on both sequence types (arbitrary and meaningful) was compared to chance by single-sample *t* test. A repeated-measures ANOVA with age as a covariate was used to determine whether performance differed on the two tasks (arbitrary and meaningful). The effects of subtype of meaningful sequence (size, color, and number) and sequence direction (ascending or descending) on performance were evaluated by ANOVA. Finally, paired *t* tests were used to determine whether children performed better in either the first or the second half of a testing block.

Results

Orangutans

Arbitrary and meaningful sequences versus chance

Figure 3a shows individual orangutans' performance on the arbitrary and meaningful sequences. Here, the three meaningful sequence subtypes—size, color, and number—were combined and considered in aggregate. By single-sample *t* test, one orangutan (Lucy) performed better than chance on both arbitrary and meaningful sequences, with $t(29)$ values of 5.32 and 2.86, $P < 0.001$ and $P = 0.008$, respectively; one orangutan (Bonnie) performed better than chance on arbitrary sequences only, with $t(29) = 2.40$, $P = 0.023$; and one orangutan (Kiko) performed no better than chance on either sequence type (P's > 0.10).

Arbitrary versus meaningful sequences

Paired *t* tests on the percentages of correct responses out of 30 trials were used to assess whether performance on one sequence type—arbitrary or meaningful—was higher than the other for each individual. Meaningful sequences were considered in aggregate for this analysis. For each orangutan, performance on the arbitrary and meaningful sequence types was not significantly different, with $t(29)$ values for Bonnie of 1.59, $P = 0.12$; for Kiko of -0.33, $P = 0.74$; and for Lucy of 1.94, $P = 0.063$. One

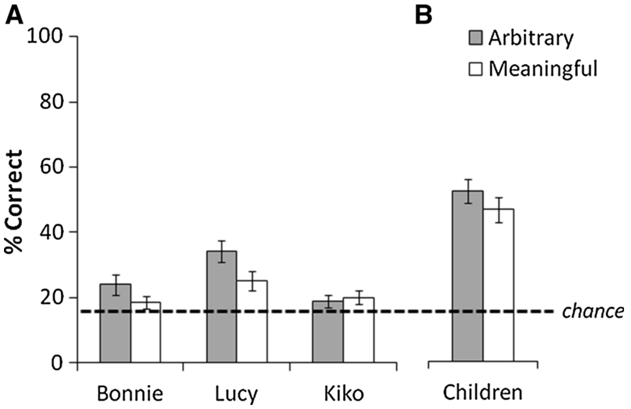


Fig. 3 Percentage of correct responses on meaningful and arbitrary sequences. **a** Overall performance by orangutans (percentage correct out of 30 trials per session). None of the three orangutans achieved significantly higher scores on meaningful than arbitrary sequences. One orangutan (Lucy) showed a nonsignificant trend toward better performance in the arbitrary task. **b** Children's overall performance (percentage correct out of 10 trials) was not significantly different on arbitrary (mean = 51.7 %) and meaningful (mean = 46.0 %) sequences. Note that means for orangutans are from repeated sessions for each individual; the means for children are group means. *Bars* indicate standard error

individual, Lucy, even showed a trend toward higher performance on arbitrary sequences (mean = 34.3 %) than on meaningful ones (mean = 25.2 %). Overall, these results indicate that orangutans did not significantly benefit from the visual cues in the meaningful sequences to improve performance relative to arbitrary sequences.

Meaningful sequences: size, color, and number

Orangutans' performance on the various meaningful sequences is summarized in Fig. 4a. Although performance on meaningful sequences overall was not different than that on arbitrary sequences, we explored the possibility that performance may have been better on at least one of the individual sequence subtypes (i.e., size, color, or number). Because performance data were not normally distributed, Friedman tests were used to determine whether individual apes achieved different scores on the various meaningful sequence types. These tests revealed that scores on the individual meaningful sequence subtypes were not statistically different from one another for Bonnie, $\chi^2(2) = 1.20$, $P = 0.55$; Kiko, $\chi^2(2) = 3.50$, $P = 0.17$; or Lucy, $\chi^2(2) = 5.84$, $P = 0.054$. In the case of Lucy, this trend was driven by high performance on color sequences and low performance on size sequences.

Ascending versus descending sequences

Orangutans were tested on both ascending and descending sequences. We evaluated whether performance on meaningful sequences was affected by the direction of the sequence by comparing ascending and descending sequences by *t* test: Bonnie and Lucy showed no difference in performance (all *P*s > 0.4), but Kiko performed significantly better on descending (mean = 24.2 %) than ascending (mean = 15.8 %) sequences, $t(28) = -2.16$, $P = 0.039$.

Item density

While two of three orangutans did not perform differently on ascending and descending sequences, we nonetheless explored whether they showed any type of bias toward a particular item in meaningful sequences. In particular, we evaluated orangutans' preference for starting with high- (largest, darkest, most numerous), medium-, and low-density sequence items (smallest, lightest, least numerous), regardless of which was the rewarded response. To address this question, we performed a 3 (density: high, medium, low) × 3 (dimension: size, color, number) within-subjects × 3 (subject: Bonnie, Lucy, Kiko) between-subjects repeated-measures ANOVA. Results revealed a significant density × dimension interaction, $F(4,22) = 3.30$, $P = 0.03$, and a main effect of density, $F(2,24) = 7.17$, $P < 0.01$. There were no other significant effects or interactions. Pairwise comparisons showed that across sessions, orangutans touched high-density items first more often than medium-density items ($P < 0.01$, Bonferroni corrected). No other comparison was significant. Planned paired *t* tests collapsing across subjects comparing the medium- and high-density items for each dimension found a significant effect only for color sequences ($P < 0.001$, Bonferroni

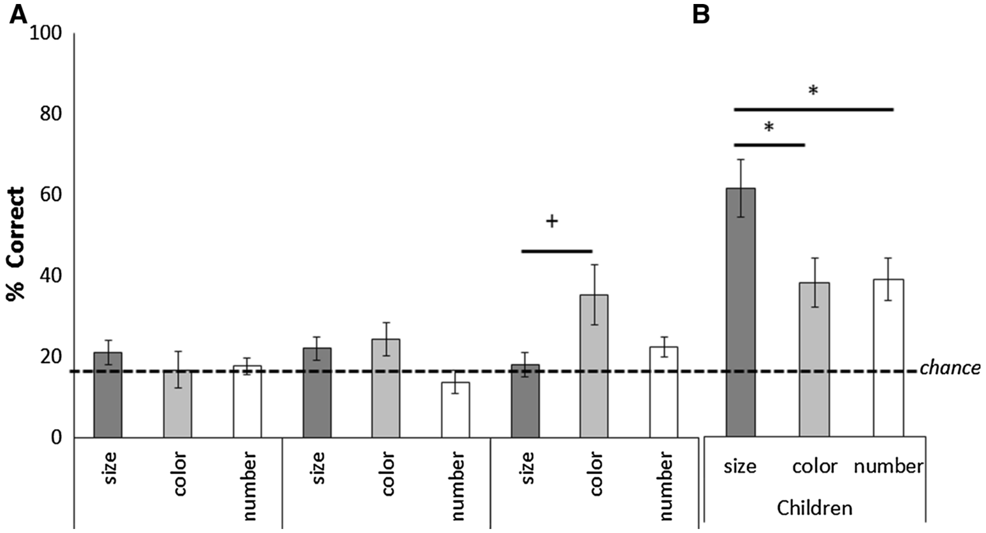


Fig. 4 Mean percentage of correct responses on sequences with specific content cues for orangutans (**a**) and children (**b**). For orangutans, performance was not significantly better for any of the individual sequence types (size, color, or number), as shown by Friedman tests. Children's performance on size lists was significantly better than that on number lists, and marginally better than that on color lists, as shown by repeated-measures ANOVA with post hoc tests. $^*P < 0.05$; $^+P < 0.10$. Note that means for orangutans are from repeated sessions for each individual; the means for children are group means. *Bars* indicate standard error

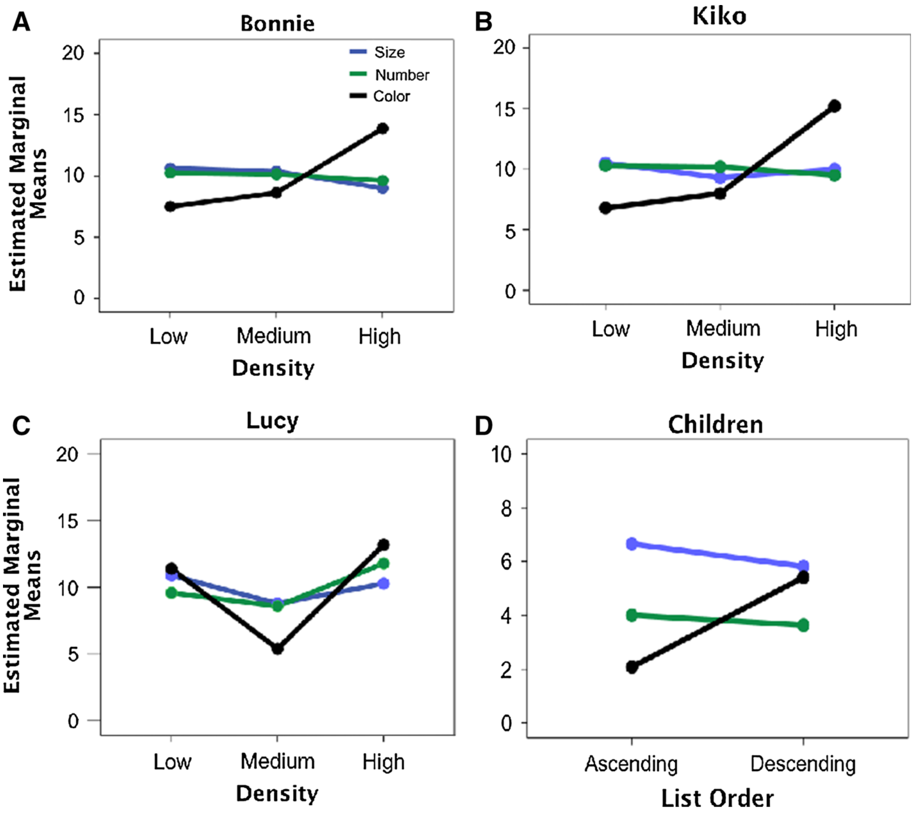


Fig. 5 Estimated marginal means for meaningful sequences. **a–c** Individual orangutans' first-item selections (out of 30 trials) based on item density regardless of ascending or descending direction. **d** Children's number of correct trials on meaningful sequences (out of 10 trials) based on direction: ascending or descending. *Blue* size, *green* number, *black* color (color figure online)

corrected). Results are summarized in Fig. 5a–c. These results demonstrate that orangutans not only discriminated between different colors, but that this discrimination biased their first response to the darkest color. However, this general preference did not significantly improve orangutans' overall performance on meaningful sequences relative to arbitrary sequences.

Effects of learning across sessions

To explore the possibility that orangutans showed improved performance over time, becoming better at learning individual sequence types, Spearman's rank-order correlations were used to determine whether there was a relationship between session number and accuracy. No significant correlations were found between session number and performance for the arbitrary sequences for Bonnie, $\rho(28) = -0.10$, $P = 0.62$; for Kiko, $\rho(28) = 0.23$, $P = 0.22$; or for Lucy, $\rho(28) = 0.28$, $P = 0.13$. For meaningful sequences, Bonnie's performance showed no significant correlation between session number and performance, $\rho(28) = -0.26$, $P = 0.17$. For Kiko, there was a weak negative relationship between session number and performance, $\rho(28) = -0.37$, $P = 0.046$. For Lucy, there was a weak positive relationship between session number and performance, $\rho(28) = 0.39$, $P = 0.032$. Taken as a whole, the results of the correlation analyses indicate that learning over time did not significantly enhance performance on later sessions for either sequence type with the possible exception of Lucy and meaningful sequences. Results are summarized in Fig. 6.

Effects of learning within a session

To investigate whether orangutans performed better in the first half or the second half of a testing block, paired *t* tests were used to compare performance (measured as the number of correct responses in the first or second half of a block). Bonnie's performance did not differ between the first and second halves of a testing block for either the arbitrary sequences, $t(28) = -1.64$, $P = 0.11$, or the meaningful sequences, $t(27) = -1.07$, $P = 0.29$. Kiko's performance likewise did not differ between the first and second halves of testing blocks for arbitrary sequences, $t(29) = -0.23$, $P = 0.81$, and meaningful sequences, $t(29) = -0.81$, $P = 0.42$. In contrast, Lucy's performance showed significant improvement between the first and second halves of testing blocks for both the arbitrary sequences, $t(29) = -4.66$, $P < 0.001$, and meaningful sequences $t(29) = -2.29$, $P = 0.029$.

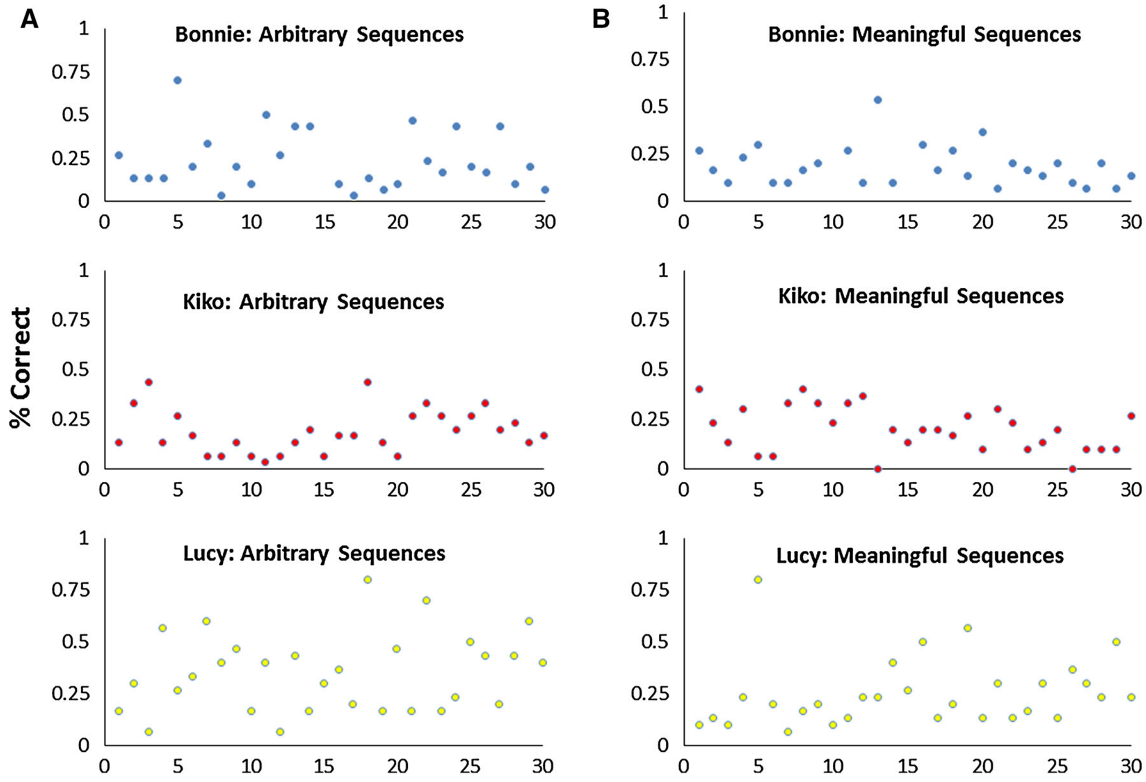


Fig. 6 Scatterplots of orangutans' performance on arbitrary (**a**) and meaningful (**b**) sequences across sessions

Children

Effects of age

According to Shapiro–Wilk's tests for normality, child age ($P < 0.01$), arbitrary correct percentage ($P = 0.01$), and meaningful correct percentage ($P < 0.01$) were not normally distributed. Therefore, Spearman's rank-order correlations were run on child age (in months) and performance (percentage of correct trials out of 10) on arbitrary and meaningful sequences. Positive correlations were found between child age and performance on arbitrary sequences, $\rho(46) = 0.33$, $P = 0.022$, as well as between child age and performance on meaningful sequences, $\rho(46) = 0.41$, $P = 0.004$. These results indicate that for both sequence types, children's performance improved with age.

Arbitrary and meaningful sequences versus chance

Children's mean performance (the number of correct trials out of 10) on arbitrary and meaningful sequences is shown in Fig. 3b. Children performed better than chance (chance = 1.67 correct out of 10 trials) on arbitrary sequences, $t(47) = 9.88$, $P < 0.001$; on meaningful sequences considered in aggregate, $t(47) = 7.68$, $P < 0.001$; and on all meaningful sequence subtypes: size, $t(15) = 6.31$, $P < 0.001$; color, $t(15) = 3.53$, $P = 0.003$; and number, $t(15) = 4.21$, $P = 0.001$ (Fig. 4b).

Arbitrary versus meaningful sequences

We used a repeated-measures ANOVA to evaluate whether children's performance was better on arbitrary or meaningful sequences, and included age as a covariate. There was no significant effect of sequence type, $F(1,46) = 0.61$, $P > 0.4$. This indicates that, like orangutans, children did not do better on either type of sequence (arbitrary or meaningful). That is, they did not benefit from the visual cues available in the meaningful sequences.

Meaningful sequences: size, color, and number

Although children's performance on meaningful sequences overall did not differ from that on arbitrary sequences, we explored whether performance differed on meaningful sequence subtypes (Fig. 4b). A two-way ANOVA was used to examine the factors dimension (size, color, number) and direction (ascending, descending) for meaningful sequences. There was a significant effect of dimension, $F(2,42) = 4.82$, $P = 0.01$, and a marginally significant dimension × direction interaction, $F(2,42) = 2.6$, $P = 0.08$. There was no main effect of direction ($P > 0.5$). Post hoc Tukey tests indicated that performance on size sequences (mean = 61 %) was significantly better than that on both color (mean = 38 %), $P = 0.025$, and number (mean = 39 %) sequences, $P = 0.03$.

Ascending versus descending sequences

The marginally significant interaction from the ANOVA reported above was further explored with post hoc tests to determine the effect of direction (ascending or descending) on performance. Performance on ascending and descending sequences was not significantly different for size or number sequences (Ps > 0.5). However, performance on descending color sequences was significantly better than that on ascending color sequences, $F(1,42) = 4.79$, $P = 0.03$.

Effects of learning within a session

Paired t tests were used to compare whether performance was different in the first and second halves of trials in a block. This was done to explore the possibility that children showed improved performance over a session, learning and remembering the individual sequence better in the last 5 trials than in the first 5. These tests showed that children performed significantly better in the second half of a block on the arbitrary sequences, $t(47) = -3.11$, $P = 0.003$, as well as on the meaningful sequences, $t(46) = -3.85$, $P < 0.001$.

Discussion

The aim of Experiment 1 was to determine whether orangutans and 3- and 4-year-old human children spontaneously use visual cues of size, color, and number to sequence three items. Generally, orangutan performance on both sequence types was much lower than that for children, even though orangutans were extensively trained and given more test trials (30 vs. 10). However, neither the orangutans nor the human children spontaneously used the visual cues to improve their performance on meaningful sequences over arbitrary sequences. That is, regardless of the species difference in overall performance, neither species showed an improvement on meaningful sequences.

Children did perform significantly better on items sequenced by size than those sequenced by number or color. However, there was a surprising result: Both children and orangutans appear to have been biased to respond first to the darkest item in a color sequence. While this bias significantly improved children's performance on descending sequences (where the starting point is the darkest color) relative to ascending sequences (where the starting point is the lightest color), it improved the performance of only one orangutan (Lucy), resulting in a nonsignificant trend toward better performance on color sequences than on size sequences. We know of no other study that has found a comparable result. Exactly why human children and orangutans have this bias is unknown.

In addition, children did better in the second half of a testing block than the first half; that is, they learned novel sequences (of either type) within a single testing block. One orangutan (Lucy) also showed better performance in the second half of a testing block than the first half for both sequence types, but the other two orangutans did not show this pattern. Only one orangutan (Lucy) showed performance improvement in later sessions on meaningful sequences.

For children, age was correlated with performance on both sequence types. That is, older children selected more correct sequences than younger children.

Experiment 2: training study with orangutans

In Experiment 1, children showed above-chance performance on both sequence types, and improvement in performance from the first half to the second half of a testing block. However, two of three orangutans did not show these patterns of performance. That is, their performance on meaningful sequences was not above chance in Experiment 1. Therefore, the purpose of Experiment 2 was to examine whether, with training, orangutans learn to use content cues when encountering novel meaningful sequences in the cognitive task. Experiment 2 was designed to discover if their overall low performance was due to an inability to sequence items by visual cue. The same general sequence types from Experiment 1 were used: (1) arbitrary sequences, in which the contents of the pictures were unrelated, and (2) meaningful sequences, in which pictures were ordered along a meaningful scale. For this study, only one scale type was used: the number of objects shown in an image. For example, a sequence of three images might have 1 → 3→ 9 arrow shapes.

Methods and materials

Participants

The three orangutans described in Experiment 1 participated in this study. This study was approved by the GWU and Smithsonian Institution IACUC. Water was available ad libitum throughout the trials, and individuals were not food-deprived before testing.

Apparatus

All training and testing were carried out with the equipment described above for Experiment 1.

Procedure

1. *Training* Training sessions consisted of 30 trials of an arbitrary sequence (the same list for every session) and 30 trials of a meaningful sequence (the same list for every session). Orangutans received training on the two sequences until they met the criterion of achieving > 65 % accuracy on each sequence three times (this could occur in different sessions). Two orangutans (Kiko and Bonnie) were trained on an ascending sequence (from few to many), and one orangutan (Lucy) was trained on a descending sequence (from many to few). One orangutan, Kiko, did not pass criterion and was dropped from the study. While Kiko was very close to achieving criterion in training for Experiment 2 (achieving 60 % accuracy in some sessions), time among other logistical constraints did not allow us to extend this experiment. Nonetheless, we are confident that Kiko would have achieved criterion had we extended the training period. Details of training for Experiment 2 are shown in Table 2.
2. *Testing* Once orangutans met criterion in the training phase, they began the experimental phase. One session comprised a block of 30 trials of an arbitrary sequence (with a new list for each session) and a block of 30 trials of a meaningful sequence (with a new list for each session), for a total of 60 trials per session. The order of arbitrary and meaningful sequence blocks was counterbalanced. Each individual completed a total of 20 sessions.

Statistical analysis

Paired *t* tests comparing performance on sequence types, as well as Spearman's correlations between session number and performance, were carried out in SPSS 19 (IBM; Armonk, NY).

Results

Paired *t* tests were run on individual ape performance data (as measured by percentage correct out of 30 trials in a session) to determine whether training on meaningful sequences (ordered by number) improved performance in novel meaningful sequences relative to novel arbitrary sequences. For both individuals, mean scores on meaningful sequences were higher than those on arbitrary ones (Fig. 7). For Bonnie, scores on meaningful sequences (mean = 59.0 %) were significantly higher than those on arbitrary sequences (mean = 21.3 %), $t(18) = -8.88$, $P < 0.001$. For Lucy, scores on meaningful sequences (mean = 68.0 %) were also significantly higher than those on arbitrary ones (mean = 34.3 %), $t(19) = -8.59$, $P < 0.001$. These results show that with training, orangutans were able to use visual cues to improve their performance on meaningful sequences.

Neither orangutan showed an improvement in performance in later sessions for arbitrary sequences as assessed by Spearman's rank-order correlation: Bonnie, $\rho(17) = 0.56$, $P = 0.14$; Lucy, $\rho(18) = 0.31$, $P = 0.19$. For the meaningful sequences, Bonnie showed a positive correlation between session number and performance, $\rho(17) = 0.75$, $P < 0.001$, which indicates that her performance on meaningful sequences improved from earlier to

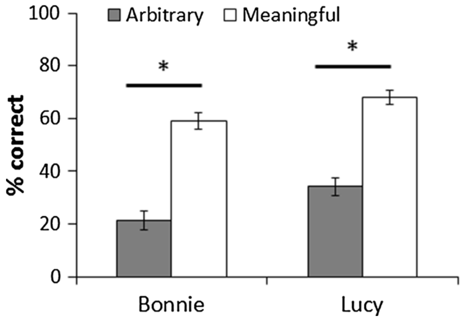


Fig. 7 Experiment 2: percentage of correct responses by orangutans on arbitrary and meaningful sequences after training on meaningful number sequences. Both Bonnie and Lucy had significantly higher percentages on the meaningful task than on the arbitrary task. *$P < 0.05$. *Bars* indicate standard error

Table 2 Orangutan participant training details for Experiment 2

Orangutan name	No. training sessions	Meaningful sequence training high score (%)	Meaningful sequence training mean score (%)	Arbitrary sequence training high score (%)	Arbitrary sequence training mean score (%)
Bonnie	24	73.33	43.9	96.67	75
Kiko	50	60	34.9	70	42.2
Lucy	17	83.33	49.0	90	72.9

later testing sessions. For Lucy, no relationship between session number and meaningful sequence performance was found, $\rho(18) = 0.34$, $P = 0.14$.

Discussion

Results from Experiment 2 showed that orangutans were able to generalize a trained rule of quantity to novel sequences with relatively little training. After training to criterion on a list ordered by number, both orangutans in this study showed significantly higher performance on novel lists organized by number than on novel arbitrary lists. These results indicate that apes, like monkeys in previous experiments (Brannon and Terrace 2000), are capable of distinguishing between items showing different quantities and ordering items in a monotonic sequence.

However, it is notable that this performance improvement over arbitrary sequences occurred only after training; orangutans did not spontaneously use the content cues of size, color, or number in Experiment 1 when ordering items in a sequence.

General discussion

These studies sought to determine whether young children and orangutans spontaneously use visual—content—cues of size, color, or number to sequence items. Overall, results showed that without prior training neither group uses these content cues spontaneously. Neither species—human or orangutan—used the available content cues to improve recall on meaningful sequences relative to arbitrary sequences. It was notable, however, that children's spontaneous performance on both meaningful (mean = 46 %) and arbitrary (mean = 51.7 %) sequences was fairly high in comparison with that of orangutans (meaningful means, 18.4–25.2 %; arbitrary means, 18.9–34.3 %).

Although performance on the meaningful sequences was not significantly different from arbitrary sequences for 3- and 4-year-old children, there was differential performance among size, color, and number subtypes (with better performance on size sequences). This result contrasts with earlier studies suggesting that children are not able to sequence items by size until later ages (Terrace and McGonigle 1994). However, the better performance on the size subtype than the number subtype is not surprising given that at ages 3 and 4, many children have not yet begun formal schooling or instruction in numbers larger than three.

An unexpected result was that whereas there was no evidence for a natural starting point for either number or size, there was a natural starting point for color. Specifically, both children and orangutans were biased to respond first to the darkest color. It is unclear why both orangutans and children showed this color-specific ordering bias. One likely explanation may have to do with the evolution of trichromatic color vision in catarrhine primates. According to a number of authors, this adaptation was driven by the need to identify fruit among foliage (Dominy and Lucas 2001) as well as a fruit's nutritional value (Lucas et al. 2003; Regan et al. 2001). This latter hypothesis for the evolution of color vision may be relevant here as the darkest color would correspond with the ripeness—and so the quality—of fruit.

Another aim of this study was to determine whether, after a training period, orangutans would begin to use visual cues to sequence novel lists of items ordered along a scale. After training, orangutans performed better on novel meaningful sequences governed by a pattern (that is, increasing or decreasing in number) than on novel arbitrary sequences. This indicates that they are indeed able to perceive and act on such content cues, but like human children require training to do so.

Although human and non-human primates are capable of sequencing both arbitrarily or meaningfully related items after a training period (D'Amato and Colombo 1988; Guyla and Colombo 2004; Swartz et al. 1991, 2000; Terrace 2001), and although monotonic sequences are easier to learn and recall than non-monotonic ones (Brannon and Terrace 2000; Ohshiba 1997; Terrace and McGonigle 1994), young human children and non-human great apes, as represented by orangutans, do not use content cues spontaneously to sequence items without some practice and training. The fact that older children (5- and 7-year-olds) use these cues readily (Terrace and McGonigle 1994), while younger children (3- and 4-year-olds) and orangutans do not, suggests that seriating items this way is a culturally learned behavior. Piaget and Inhelder (1964, chap. 9) came to a similar conclusion. They also argued that preschool-age children do not spontaneously use perceptual cues to seriate items. They went on to argue that only after children have started sorting items based on these cues themselves can they recognize these cues and organize items accordingly on their own. One possible exception noted above might be color; however, future studies are necessary to specifically address that question.

Although neither group tested here improved their performance by using visual cues, the children achieved overall higher percentages of correct responses than the orangutans. Why might humans show an early aptitude for sequential behaviors, regardless of the type of content cue involved? Such behaviors are likely linked to various aspects of human culture, including rituals and language use, both of which require the systematic combination of responses (sounds—phonemes and morphemes—or actions and gestures) in a particular order.

One potential limitation of this study is that surface area and object number were confounded in the stimuli ordered by number, and surface area and size were confounded in the stimuli ordered by size. However, previous studies showed that number-naïve monkeys do distinguish between surface area and number (Cantlon and Brannon 2007) and can match samples based on either dimension. In order to gauge spontaneous solutions of these sequences, we intended the task to be as transparent as possible for novice participants. When primates have been previously trained to distinguish numerical items designed not to confound number and surface area, hundreds to thousands of training trials have been required (Brannon and Terrace 2000). Regardless of this relationship between surface area, size, and number, it is clear that orangutans, generally, do not use any of these cues spontaneously to solve sequencing problems, though the nonsignificant trend displayed by one orangutan for color sequences is of interest and merits follow-up study.

Another potential limitation of the present study is that by initially training apes exclusively on arbitrary sequences, we may have inadvertently trained them to ignore meaningful cues (as there were none in the arbitrary sequences). This bias may have been exacerbated by the fact that we presented apes with multiple different types of meaningful sequences in Experiment 1. Arguably, one reason why apes might have performed better on meaningful sequences in Experiment 2 but not in Experiment 1 may have been that the differences between the meaningful sequences were smaller (because they were all of the same type) than in Experiment 1. Of course, prior to testing in Experiment 2, we trained the apes on a single meaningful sequence until they reached a high performance criterion, essentially training their attention on the meaningful cues. In the opinion of the authors, this latter account best explains the apes' performance in Experiment 2.

While using both ascending and descending sequences in Experiment 1 may have made the task more challenging for the orangutans, using a single sequence direction (e.g., always ascending) might have implicitly trained orangutans' perceptual attention, resulting in a generic behavioral response that could be applied across sequences. To avoid this potential confound, we used both ascending and descending sequences between sessions. This procedure allowed us to assess whether orangutans could spontaneously as well as flexibly order sequence items across different dimensions. Experiment 2 makes clear that once sequence direction as well as the cue (e.g., numerosity) is held constant, orangutans attend to these cues.

Future research with non-human primates may address whether orangutans are representative of other apes, or whether other ape species would perform differently on this task. Additionally, it will be important to address whether apes might more easily seriate ecologically relevant items such as food quantities or dominance hierarchies in addition to ecologically valid colors such as reds and greens. Future studies with images that include food items such as fruits and leaves may shed further light on this possibility. Future research with humans may be directed to the question of why children do fairly well on tasks like this, even without the benefit of content cues. Is this related to the nature of the task; that is, would they perform as well if the items were three-dimensional physical objects rather than images on a touchscreen? In addition, future studies can determine the age at which children spontaneously begin sequencing items by size, color, or number. Is this related to cultural practices such as formal education and experience in school with naming or seriating numbers, sizes, and colors? If so, might children from cultures that lack formal education fail to spontaneously order by size or number? Answers to these questions may ultimately shed light on a fundamental aspect of human cognition, one that almost certainly underlies skills such as language and ritual that are presumed to be uniquely human.

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Compliance with ethical standards

The portion of the research involving human children was approved by the George Washington University Institutional Review Board. All procedures performed in studies involving human participants were in accordance with the ethical standards of the IRB and with the 1964 Helsinki Declaration and its later amendments or comparable ethical standards. The portion of the research involving orangutans was approved by the George Washington University IACUC and Smithsonian Institution ACUC. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution at which the studies were conducted.

Conflict of interest The authors declare that they have no conflict of interest.

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