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Extraction of Structural Regularities by Baboons (*Papio papio*):

Adjacent and Non-adjacent Repetition Patterns Differ in Learnability

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Abstract

Several animal species can discriminate between different sequential patterns based on repetitions of items (e.g., ABB *versus* ABA), and generalize their performance to sequences made of novel elements but following the same underlying structure. This achievement suggests that these species possess the ability to abstract the sequences structures beyond exemplars. Developmental studies in humans suggest however that adjacent repetition patterns (e.g. ABB) are easier to extract than patterns based on a non-adjacent (e.g., ABA) repetitions. This study addressed this effect of adjacency from a comparative perspective. Seventeen Guinea baboons (*Papio papio*) were tested with an adaptation of the serial response time task. In Experiment 1, baboons exposed to adjacent or non-adjacent repetition patterns showed shorter response times in responses to novel adjacent and non-adjacent repetition sequences compared to random sequences, suggesting successful generalization of both patterns. In Experiment 2, sequences of the form ABB, ABA and ABC were presented at equal frequencies to test whether baboons would be sensitive to repetitions under these conditions. Response times were faster for adjacent repetitions (ABB) than in the two other conditions. Overall, these results suggest that baboons are sensitive to both adjacent and non-adjacent repetition patterns, but also confirm in baboons that adjacent repetitions are more salient than non-adjacent repetitions.

Key words: rule learning, artificial grammar learning, pattern learning, monkey

Introduction

When reading the following three-syllable sequences, « ga ti ga » and « li na li », we can memorize each of them individually, but can as well notice that they share a common structure: their first and last syllables are identical while their second syllable differs. The extraction of such an « ABA » pattern requires the processing of the structural properties of the sequences beyond the exemplars, allowing generalization to novel, isomorphic sequences. In humans, sensitivity to the structural organization of words within sentences has been proposed as one of the core mechanisms underlying the formation of grammatical knowledge (e.g., Gomez & Gerken, 1999; Marcus, Vijayan, Rao, & Vishton, 1999). The comparative study of this ability therefore offers an entry into the assessment of non-human animals' syntactic abilities.

The extraction of sequential patterns has been extensively studied in laboratories using AAB, ABB and ABA patterns based on repetitions. In the AAB/ABB patterns, there is an immediate repetition of an item within the triplet (« adjacent repetition patterns »). In the ABA pattern, the first and last elements of the triplets are identical, while the element in the middle differs (« non-adjacent repetition pattern »). In a seminal experiment conducted by Marcus, Vijayan, Rao, and Vishton (Experiments 1 and 2, 1999), seven-month-old infants were exposed to triplets of syllables following either an ABB or ABA pattern (e.g., « ga ti ti », « ga ti ga », respectively). They were then tested with pattern-following sequences, and pattern-violating sequences made of novel syllables of the form ABA for the group exposed to ABB sequences (e.g., « wo fe wo »), and *vice-versa*. Infants from both groups showed preference for pattern-violating sequences compared to pattern-following ones, suggesting that they were able to learn and generalize the underlying structures.

An extensive number of studies was conducted to assess pattern learning abilities in nonhuman species, following Marcus et al. (1999). Most of these studies used operant conditioning procedures. With these procedures, the subjects are typically first trained to discriminate two different repetition patterns in a Go/No-go (e.g., Murphy, Mondragón, & Murphy, 2008) or a two-alternative forced choice task (e.g., Santolin, Rosa-Salva, Regolin, & Vallortigara, 2016). Individuals are then tested with generalization trials involving sequences made of novel stimuli.

Convincing generalization performance was obtained in several species with that procedure, participants showing correct discrimination in generalization trials. In rodents, rats could discriminate an AAB pattern from random ABC sequences, with the A and B items being either vowels (Experiment 1) or consonants (Experiment 2) presented in auditory sequences, and transferred this knowledge to novel phonemes (*Rattus norvegicus,* de la Mora & Toro, 2013; see also Murphy et al., 2008). In birds, Spierings & ten Cate (2016) have shown that budgerigars (*Melopsittacus undulatus*) can discriminate sequences of song elements of the form AAB and ABA and generalize their performance to sequences constructed with a novel set of songs. Chicks also successfully discriminated ABA and ABB patterns, as well as ABB and AAB patterns, in a task relying on a non-sequential presentation of strings of visual shapes (*Gallus gallus*, Santolin, Rosa-Salva, Regolin, & Vallortigara, 2016; see also Versace, Spierings, Caffini, ten Cate, & Vallortigara, 2017). In an experiment using a similar procedure, two chimpanzees correctly generalized an AB^{n}A pattern to novel colors and shapes (with one to five intervening B elements; *Pan troglodytes,* Sonnweber, Ravignani, & Fitch, 2015; see also Ravignani & Sonnweber, 2017). Finally, cotton-top tamarins respond differentially to novel pattern-following and pattern-violating sequences (AAB vs. ABB) made of speech elements or tones (*Saguinus oedipus,* Neiworth et al., 2017). All these data suggest that the ability to discriminate between different patterns, based on initial adjacent repetition (AAB), final adjacent repetition (ABB), and non-adjacent repetition (ABA) is widespread among animal species.

These studies, however, convey at least one limitation, as none of them has assessed whether those different repetition patterns differ in learnability. Notably, one possibility would be that patterns based on an adjacent repetition are easier to process than a pattern based on a non-adjacent repetition. Discrimination tasks contrasting one repetition pattern against another (e.g. AAB *vs*. ABA) are not suitable to assess this question, as participants can perform the task by processing only one pattern (e.g., by detecting the presence/absence of an immediate repetition; ten Cate & Okanoya, 2012; Corballis, 2009), without processing the full structure underlying the other pattern(s). To solve this problem, researchers working with humans have for instance added random ABC sequences in their designs, and therefore contrasted ABA and ABB patterns against ABC sequences. This procedure revealed that the ability to process adjacent and non-adjacent repetition patterns follow different developmental trajectories, the former appearing earlier than the latter (Gervain, Macagno, Cogoi, Pena, & Mehler, 2008; Gervain & Werker, 2013; see also Johnson et al., 2009; Kovács & Mehler, 2009). One study suggests that this difference in learnability can also be found in birds (van Heijningen et al., 2013, Experiment 1). These authors trained zebra finches to respond to ABA (S+), but not to AAB/ABB (S-) sequences in a Go/No-go task. Probe tests involving sequences such as ABBA have suggested in this study that the finches responded by attending to the presence/absence of adjacent repetitions only. Therefore, it seems that the extraction of adjacent repetition patterns is easier than the extraction of non-adjacent repetition ones, but evidence from comparative studies remain scarce.

The aim of the current experiments was therefore to further assess to what extent adjacent repetition patterns may differ in learnability from a non-adjacent repetition pattern. For this purpose, we assessed the sensitivity of non-human primate species, the Guinea baboon (*Papio papio*), to each kind of repetition pattern. Experiment 1 assessed baboons' ability to learn and generalize those patterns. Our group of participants was of baboons split in two halves. One group was exposed to sequences following an adjacent repetition pattern, and the other group was exposed to sequences following a non-adjacent repetition pattern. We then tested their ability to discriminate each repetition pattern against random sequences (for a similar approach with humans, see Gervain & Werker, 2013, Experiment 1). After completing those tests, the groups were tested on the other pattern. This procedure allowed us to assess baboons' sensitivity to each pattern, successively and in the same task and in the same individuals. In Experiment 2, adjacent repetition (ABB), non-adjacent repetition (ABA) and random (ABC) patterns were presented at equal frequencies, to test whether baboons would be sensitive to adjacent and non-adjacent repetitions under these conditions, only to the former, or to none of them.

Experiment 1

Experiment 1 aimed at testing baboons' ability to learn and generalize an adjacent (AA) and a non-adjacent repetition pattern (ABA) by contrasting these patterns with random sequences (AB and ABC, respectively). The baboons were first exposed to sequences of visual shapes instantiating each kind of repetition pattern, and then tested on sequences made of novel shapes either following or violating (random sequences) the repetition pattern.

Methods

Subjects and apparatus

Participants were 17 Guinea baboons (*Papio papio*, 11 females, age range 4-21 years). Six other baboons were tested but not included because they did not complete the experiment within the time allowed to this experiment. The baboons live within a larger group of individuals, within a 700 m2 outdoor enclosure and had permanent access to ten Automated Learning Devices for Monkeys (ALDM, for a detailed description, see Fagot & Bonté, 2010; Fagot & Paleressompoulle, 2009), each equipped with a 19-inch touch screen and a food dispenser. The main feature of ALDM equipment is that a radio frequency identification reader (RFID) identifies each baboon via microchips implanted in their arms. The baboons can therefore participate to research at will, as the test programs recognize the individuals automatically. The experiment was controlled by the EPrime software (Version 2.0, Psychology Software Tools, Pittsburgh).

Prior to the experiment, the baboons have never been tested on sequential pattern learning, but they had participated in numerous computerized experiments using the ALDM test systems, including some experiments on statistical learning, involving chunking of triplets of stimuli (Minier, Fagot, & Rey, 2016), and learning of non-adjacent dependencies (Malassis, Rey, & Fagot, 2018).

Stimuli

They were 192 different yellow visual shapes (available in Supplementary Information) selected from the Unicode 9.0 repertoire considering their apparent discriminability. Each shape measured 180x180 pixels maximum.

Task and test procedure

We used an adaptation of the serial response time task (SRT, Nissen & Bullemer, 1987), inspired from Misyak, Christiansen, and Tomblin (2010). This task involves self-paced presentation of sequences of cued stimuli in which response times (RT) provide a continuous measure of the participants' expectations about the incoming stimulus. In this task, RTs are expected to become increasingly fast throughout exposure, if participants are sensitive to the sequences structure. By contrast, they should slow down if a sequence violating this structure is encountered.

Figure 1 illustrates the procedure used in each trial. A trial (see Figure 1) began by the display of a fixation cross (120x120 pixels) presented at the bottom of the screen. Touching this stimulus triggered the display of two shapes, presented one above the other (upper/lower location balanced) on the left side of the screen. One of the two shape was surrounded by a square (empty fill, white border; hereafter “cue”) which served to designate the positive stimulus (S+) that the baboon had to touch. The square appeared around S+, and then disappeared from the screen after 350 ms, in contrast to the two stimuli which remained on the screen until the subject touched one of them. A correct touch of S+ immediately triggered the display of a second pair of shapes. Presentation of this second pair of shapes used the same procedure (for shape and cue presentation) as for the first pair, but the two stimuli were now presented on the right side of the screen, and the cue appeared around S+ after a delay of 100 ms. A correct selection of S+ in this second display delivered grains of dry wheat. An incorrect selection of S- on either the first or the second display immediately stopped the trial and triggered a 3-sec timeout without food reward. The baboons could respond to each pair of shapes during or after the appearance of the cue. Trials in which the baboon failed to select a stimulus within five seconds (from trial onset) were aborted and presented again immediately. The procedure outlined above was followed for the presentation of the adjacent repetition pattern. It was also used for presenting the non-adjacent repetition pattern, with the exception that these trials involved three instead of two displays, which were presented sequentially in left, center and right part of the screen.

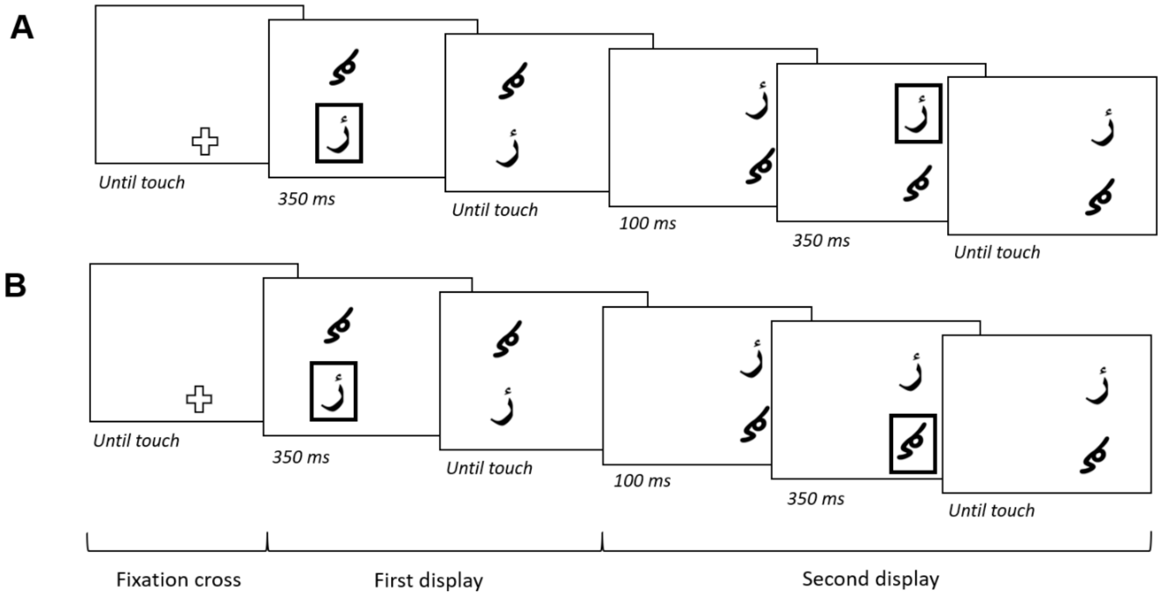

Figure 1. Timeline of a trial in Experiment 1. A. Trial presenting an adjacent repetition pattern-following sequence (of the form AA). B. Pattern-violating sequence (of the form AB).The task was similar for non-adjacent repetition trials, except that three instead of two displays were presented.

Our procedure aimed at comparing baboons' responses to repetition patterns to their responses to random sequences. Figure 2 provides an overview of the experiment timeline. The baboons were tested with the two repetition patterns, one after the other, in a within-subjects design (order counterbalanced across participants; Group 1: n = 9, Group 2: n = 8). For each pattern, the baboons performed three phases: an exposure phase, a generalization test, and a violation test. These phases were presented sequentially, and the order of the two test phases was counterbalanced across baboons. Our collection of 192 shapes was divided in six sets of 32 shapes each (see Supplementary Information). Each set served to generate the sequences for a given phase and pattern. The sets involved in generalization and violation phases were counterbalanced across baboons. Table 1 provide a summarized description of the phases and conditions involved in Experiment 1.

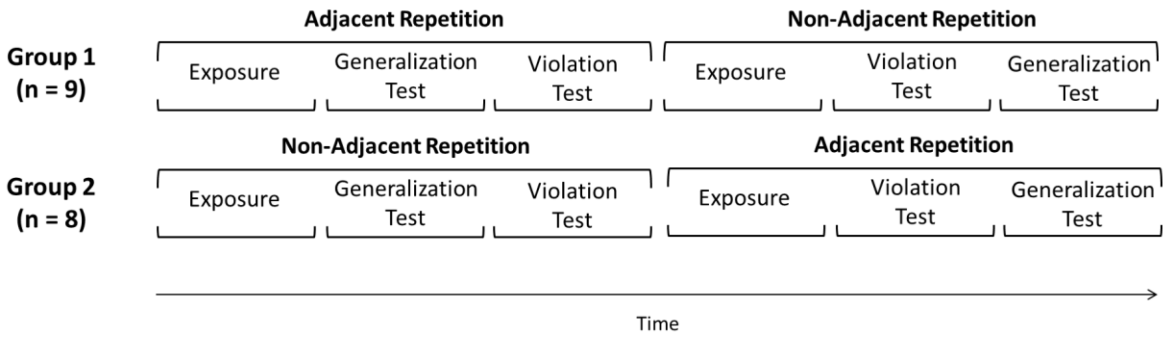

Figure 2. Timeline of Experiment 1. The two pattern experiments (adjacent repetition, non-adjacent repetition) were conducted one after the other, their order being counterbalanced across participants. The order of the test phases was also counterbalanced across participants within each pattern experiment.

Two types of sequences were presented to the baboons during the exposure phase: baseline (95% of the trials) and violation (5%) sequences. For the adjacent repetition pattern, baseline sequences were of the form AA, and violation sequences were of the form AB, with the A and B stimuli being drawn from the same set of shapes. For the non-adjacent pattern, these two types of sequences were of the form ABA and ABC, respectively, A, B and C stimuli being all drawn from the same set of shapes. In violation trials, the cue appeared around the distractor (i.e., around “B” instead of “A” for the adjacent repetition pattern, and around “C” instead of “A” for the non-adjacent repetition pattern). Baboons were expected to select the cued stimuli. Because 95% of the sequences followed an adjacent or a non-adjacent repetition pattern, it was possible to predict the stimulus to be selected in the last display. Patterns learning therefore predicts a decrease in RTs on the last stimulus of baseline sequences throughout exposure. The introduction of a small amount of violation sequences aimed at disentangling learning of repetition patterns from a mere effect of task practice. We assumed that repetition pattern learning will be indicated by slower RTs on violation trials compared to baseline trials.

During the test phases (i.e., the generalization and violation tests), sequences of novel shapes were presented in 20% of the trials. In the generalization test, these sequences followed the repetition pattern. In the violation test, these were random sequences (i.e., of the form AB for adjacent pattern, and ABC for non-adjacent repetition pattern). The remaining 80% of the trials were baseline sequences, randomly intermixed with the novel sequences. Reinforcement schedules were similar to those of the exposure phase: baboons were expected to select the cued stimuli and were reinforced to do so. Note that novel pattern-following and pattern-violating sequences were presented at similar frequencies in generalization and violation tests, respectively. Rote learning of the novel sequences therefore predicts no difference in RTs between tests, while generalization of the learned patterns predicts slower RTs in the violation compared to the generalization test.

For each pattern, the exposure phase involved 25 sessions of 160 trials (five repetitions of each shape as S+ within a block), and each test phase involved five sessions of 160 trials (four repetitions of each exposure shape and one presentation of each novel shape as S+ within a block). To complete the experiment, the baboons required 18 days on average (range 10-26). Custom-written Python codes (www.python.org) were used to generate the sequences.

Table 1 Description of the phases and conditions involved in Experiment 1

Pattern	Phase	Condition	Sequences Structure	Percentage of Trials	Stimulus Set (n°)
Adjacent Repetition	Exposure	Baseline	AA	95%	1
		Violation	AB	5%	
	Generalization Test	Baseline	AA	80%	1
		Generalization	AA	20%	2 or 3
	Violation Test	Baseline	AA	80%	1
		Violation	AB	20%	2 or 3
Non-Adjacent Repetition	Exposure	Baseline	ABA	95%	4
		Violation	ABC	5%	
	Generalization Test	Baseline	ABA	80%	4
		Generalization	ABA	20%	5 or 6
	Violation Test	Baseline	ABA	80%	4
		Violation	ABC	20%	5 or 6

Note that the stimulus sets used in the test phases were counterbalanced across participants. Stimuli used in the different sets are available in *Supplementary Information*.

Data analyses

In the current design, the short delay (100 ms) before the appearance of the cue is too short to allow the participants to respond before the cue. Therefore, we do not expect the baboons to make more errors in violation trials compared to baseline or generalization trials. This was confirmed by our data: the proportion of errors remained low on average (5.76%) and did not distinguish violation from generalization trials. Statistical analyses were therefore restricted to RTs. With this test design, the analyses focused on the responses times obtained for touching the stimulus in the last display (i.e. the second display for adjacent repetition pattern, and the third display for non-adjacent repetition pattern). RT corresponded to the time elapsed between the appearance of the stimuli from the last display and the participant's selection of one of the two shapes. Incorrect trials were removed from the data set as well as trials with any abnormally long RT (i.e., with a RT > 3 s on at least one display; 0.22% of the trials). Sessions were grouped in five (Exposure) and two (Test) blocks of 800 trials each for statistical analyses. Statistical analyses were done with R (V3.1.1, www.R-project.org).

Learning during the exposure phase was first assessed by comparing baboons' RTs on baseline and violation trials, for each pattern. This was evaluated with a repeated-measures ANOVA involving the Condition (Baseline, Violation), Pattern (Adjacent, Non-adjacent) and Block (1-5) as within-participant factors. Post-hoc comparisons were performed using Tukey's HSD test ($p < .05$).

Two statistical analyses were conducted on the test phases. The first one aimed at verifying that baboons discriminated the novel shapes from the shapes used in baseline sequences, which predicts an increase in RTs. One-sided paired t-tests assessed whether the RTs were greater for the novel compared to baseline sequences. The second analysis assessed whether the increase in RTs (if any) was greater for violation sequences, compared to the generalization sequences. For each participant, mean difference in RTs between the novel and the baseline sequences was computed for each test. These data were then analyzed using one-sided paired t-tests.

Results and Discussion

Exposure phase

Mean RTs are reported in Figure 3 for each pattern, condition and block. The main effect of condition was significant, $F(1, 16) = 15.95$, $p = .001$, partial $\eta_p^2 = .50$, corresponding to overall faster RTs in the baseline (Mean ± SD = 512 ± 50 ms) than in the violation condition (533 ± 69 ms). Also significant was the main effect of Block, F (1, 16) = 17, $p <$ .001, partial $\eta_p^2 = .52$, showing that RTs decreased with practice. No main effect of Pattern was found, F (1, 16) = 0.03, $p = .87$ (adjacent repetition pattern: 524 ± 58 ms; non-adjacent repetition pattern: 521 ± 64 ms). A significant Condition x Pattern interaction was however found, F (1, 16) = 7.31, $p = .02$, partial $\eta_p^2 = .31$. Post-hoc tests revealed that mean RTs for the different types of sequences differed significantly from each other, in the following order: AA (507 ± 43 ms) < ABA (516 ± 57 ms) < ABC (527 ± 71 ms) < AB (540 ± 67 ms). No other interaction was found (all *p*s > .44). This significant increase in response time observed on the violation sequences for the adjacent and non-adjacent repetition patterns suggests that baboons successfully learned both repetition patterns. However, baboons showed differential responses to the two patterns: effect size of the difference between baseline and violation conditions was moderate to high for the adjacent repetition pattern (Cohen’s $d = 0.58$) and small for the non-adjacent repetition pattern ($d = 0.17$). Further, baboons were faster to respond to baseline sequences of the adjacent repetition pattern than of the non-adjacent pattern, and showed their slowest RTs in reaction to violations of the former.

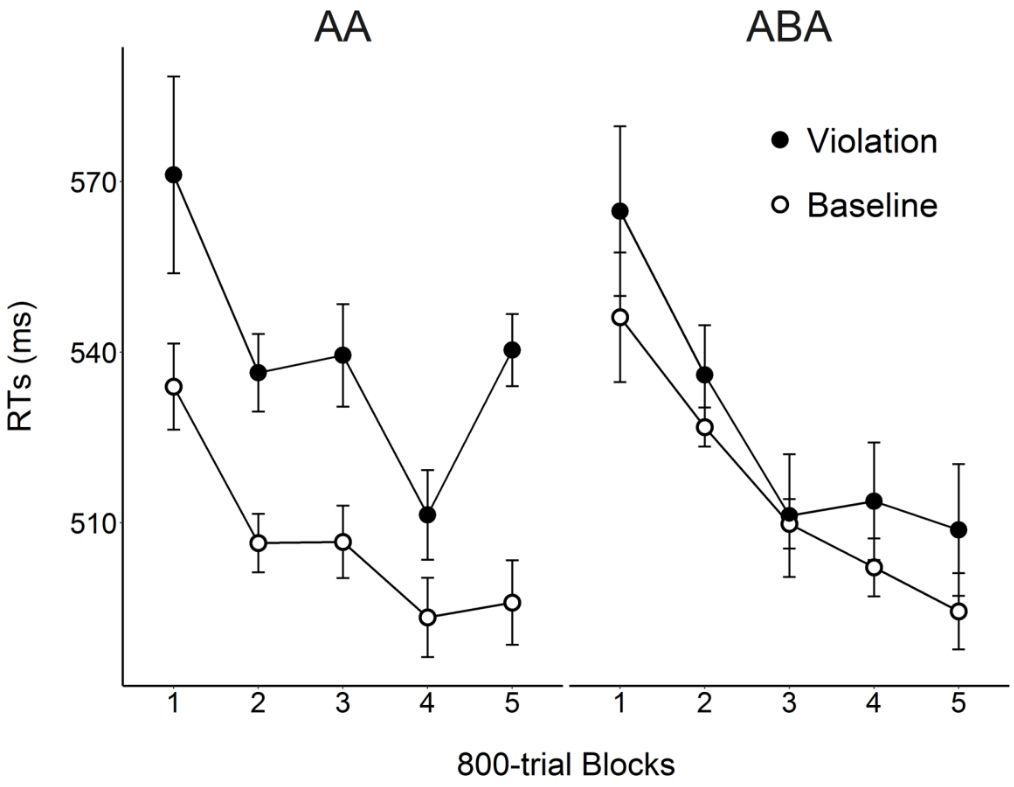

Figure 3. Response times (RTs) obtained in the exposure phase of Experiment 1. Left: adjacent repetition pattern; right: non-adjacent repetition pattern. Bars represent standard errors after subtraction of the individuals' mean RTs.

Test phases

Mean differences in RTs between the novel and baseline sequences are reported in Figure 4 for each pattern and test. A significant positive difference was observed for every pattern and test type: for the adjacent repetition pattern, RTs were greater in generalization trials compared to baseline trials of the generalization test (M ± SD = 538 ± 68 ms, and 487 ± 33 ms, respectively, t (16) = 4.01, p < .001, Cohen's d = 0.96), as well as in violation trials compared to baseline trials of the violation test (569 ± 61 ms, and 486 ± 37 ms, respectively, t (16) = 6.31, p < .001, d = 1.64). For the non-adjacent repetition pattern, a similar increase in RTs was observed (generalization *vs* baseline trials of the generalization test: 535 ± 54 ms, and 500 ± 36 ms, respectively, t (16) = 4.66, p < .001, d = 0.76; violation *vs* baseline trials of the violation test: 542 ± 51 ms, and 492 ± 33 ms, t (16) = 6.01, p < .001, d = 1.18). These results confirmed that the baboons discriminated the novel shapes used to construct the generalization and violation sequences from the shapes instantiating baseline sequences.

We then assessed whether this difference in RTs was greater for the violation compared to the generalization test. A significant difference was found for the adjacent repetition pattern (Mean difference ± SD = 83 ± 54 ms, and 52 ± 53 ms, respectively, t (16) = 2.75, *p* < .01, *d* = 0.60), as well as for the non-adjacent repetition pattern (50 ± 34 ms, and 35 ± 31 ms, respectively, t (16) = 2.12, *p* = .03, *d* = 0.48).

In sum, all the data reported above suggest successful extraction and generalization of both adjacent and nonadjacent repetition patterns, as indicated by baboons' shorter RTs on the last element of generalization sequences compared to the RTs obtained on the same element in violation sequences.

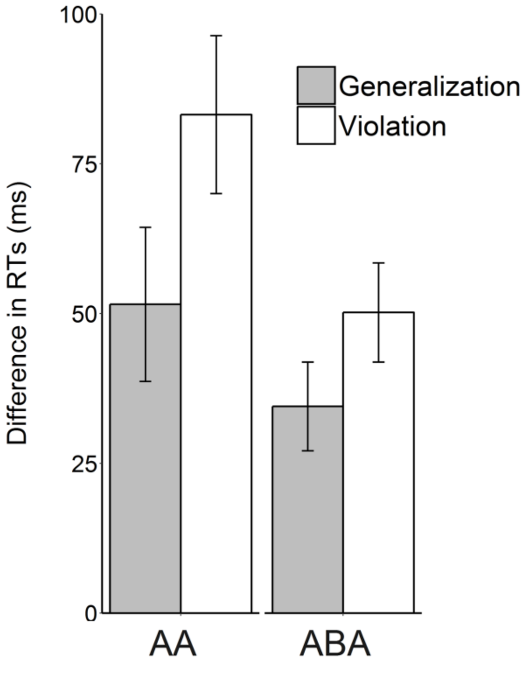

Figure 4. Mean response times (RTs) difference between the novel and baseline conditions of each test phase of Experiment 1. Left: adjacent repetition pattern; right: non-adjacent repetition pattern. Positive values indicate longer RTs in the novel condition compared to the baseline condition. Bars represent standard errors.

Experiment 2

Experiment 1 has suggested that the baboons learned and generalized both adjacent and non-adjacent repetition patterns. However, the possibility remains that RT differences observed between the repetition and random sequences derived from the novelty of the last element within this last type of sequences. Moreover, one limitation of the first experiment is that it involved sequences of different lengths for the adjacent repetition and non-adjacent repetition patterns (two and three items, respectively). Those issues were addressed in Experiment 2. This second experiment used three-item sequences following an adjacent repetition pattern, a non-adjacent repetition pattern, or a random pattern (of the form ABB, ABA, and ABC, respectively). Those three types of sequences were presented at equal frequency. This procedure aimed as assessing whether baboons would show sensitivity to repetitions even under those conditions. Six months elapsed between the two experiments, during which the baboons were exposed to different and unrelated tasks.

Methods

Subjects, stimuli and task

Data were collected on a total of 13 baboons (six females, age range 4-21 years). Among them, nine had participated in Experiment 1. Eleven other baboons were tested but not included in the analyses because they did not complete the experiment in the allotted time. The apparatus was the same as in the previous experiment.

Experiment 2 used 32 different shapes which have served previously to construct test sequences in Experiment 1 (Set 6). The use of shapes already presented in test sequences was not problematic in itself, because the low frequency of these sequences in Experiment 1 (five repetitions) prevented their learning.

In Experiment 2, the cue was no longer a square surrounding the positive stimulus (S+). It was instead a short disappearance of the stimulus giving the impression that it blinks once. This change was introduced because another experiment (Fagot, Malassis, & Medam, 2017) suggested that baboons' attention to the task was increased with this procedure. On each display, the two shapes were first presented during 200 ms, after which the S+ disappeared for a short period of 80 ms. The two shapes then remained displayed on the screen until the participant touched one of them. Spatial and temporal parameters of the trials were identical to Experiment 1.

Procedure

Three 3-shapes patterns were presented to the baboons at equal frequencies: random pattern (ABC), pattern involving a final adjacent repetition (ABB) and pattern involving a non-adjacent repetition (ABA). A, B and C stimuli were all drawn from the same set of 32 shapes (Set 6). Ninety-six sequences were created for this design. Thirty-two A-B pairs of shapes were chosen pseudo-randomly, and used as sequences' beginning for the three patterns. They were followed at equal frequencies by an A, B or C shape, rendering the third shape unpredictable (i.e. with a probability of 0.33 in each case). The frequency of each shape within each position was balanced among the three patterns. Experiment 2 involved a total of ten sessions of 96 randomly intermixed trials. Each session comprised 32 sequences for each of the three patterns described above. The 13 baboons required 3.5 days on average to complete Experiment 2 (range 1-6).

Results and Discussion

Sessions were grouped for the analysis in five blocks of 192 trials each. Incorrect trials were removed from the data set (35 %), as well as trials with any abnormally long RT (i.e., with a RT > 3 s on either the first, second or third target; 0.5%). Analyses were conducted on baboons' RTs for touching the stimulus in the last display (i.e., the time elapsed between the apparition of the last stimulus and the participant's touch). Mean RTs are reported in Figure 5 for each pattern and block. A two-way repeated-measures ANOVA revealed a main effect of Pattern, F (2, 24) = 11.79, $p < .001$, partial $\eta_p^2 = .50$. Tukey's HSD test indicated significantly faster RTs for the ABB pattern (M ± SD = 660 ± 66 ms) compared to the ABA (715 ± 77 ms, Cohen's $d = 0.76$), and ABC patterns (707 ± 62 ms, $d = 0.72$). No significant difference was observed between the ABA and ABC patterns ($p = .41$). The main effect of block was close to significance, F (1, 12) = 3.90, $p = .07$, partial $\eta_p^2 = .50$, as was the Pattern x Block interaction, F (2, 24) = 2.55, $p = .10$, partial $\eta_p^2 = .50$, suggesting greater acceleration throughout the task for the ABB pattern, compared to the two others.

To analyze the response times obtained at the onset of the experiment, we computed two-tailed paired t-tests comparing the mean RTs obtained in the ten first trials for the different patterns. These analyses indicated a tendency for shorter RTs for the ABB pattern (689 ± 90 ms) than for both the ABA pattern (729 ± 123 ms), t (12) = 1.86, $p = .09$, $d = 0.37$, and the ABC pattern (723 ± 67 ms), t (12) = 1.89, $p = .08$, $d = 0.43$. Here again, no difference was found between the ABA and ABC patterns, t (12) = 0.20, $p = .84$.

These results therefore suggest an initial speed advantage for the adjacent repetition pattern (ABB), which increased throughout the experiment. The acceleration observed for the adjacent repetition pattern, but not for the two others, suggests that repeated exposure to adjacent repetitions may prompt their subsequent recognition, even when their probability is equated with other types of sequences (the last element being a repetition of either the first or second shape, or being new, with a probability of .33). Conversely, no difference in RTs was found between ABA and ABC patterns, revealing that baboons show sensitivity to adjacent repetitions only under those conditions.

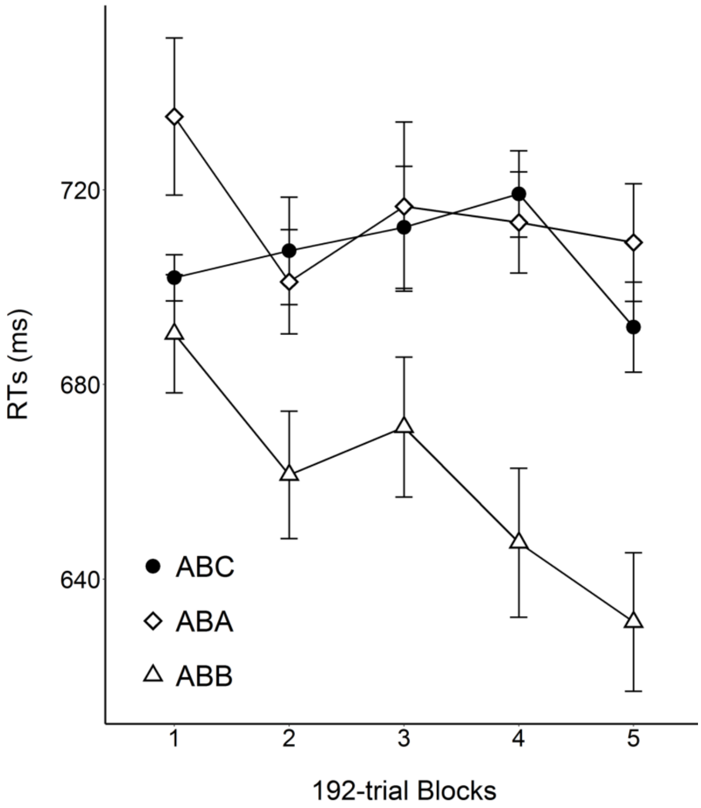

Figure 5. Response times (RTs) for each pattern across blocks in Experiment 2. Bars represent standard errors after subtraction of the individuals' mean RTs.

General Discussion

In Experiment 1, baboons' response times were longer for random sequences compared to adjacent and non-adjacent pattern-following sequences, whether the sequences were made of familiar (during exposure phase) or novel shapes (test phases). Earlier studies supporting this conclusion contrasted ABA against AAB (and/or ABB) repetition patterns (e.g. Santolin et al., 2016; Spierings & ten Cate, 2016). However this comparison is unable to rule out the hypothesis that the participants performed the task only by processing the adjacent repetition pattern, and treating the other by exclusion (e.g. ten Cate & Okanoya, 2012; Gervain & Werker, 2013). The main strength of our research is to contrast each repetition pattern against random sequences. The current data therefore confirm that baboons' pattern learning abilities are not restricted to patterns based on adjacent repetition. Baboons are also sensitive to non-adjacent repetition patterns, at least when those patterns are not interleaved with sequences containing adjacent repetitions.

In the second experiment, however, baboons show sensitivity to adjacent repetitions only. One critical feature of Experiment 2 is that the three types of patterns were presented at equal frequencies. This result confirms that adjacent repetition are more salient for baboons than non-adjacent repetitions, in line with previous results obtained in human infants (e.g., Gervain et al., 2008; Gervain & Werker, 2013; Johnson et al., 2009).

One possible explanation for baboons' lack of sensitivity to non-adjacent repetitions in Experiment 2 is that they may have focused exclusively on adjacent repetition. Indeed, the presence of adjacent repetitions may impede the exploitation of more complex structural regularities. The current results are reminiscent of two comparative studies aimed at studying birds' ability to discriminate sequences of the form A^nB^n from sequences of the form $(AB)^n$ (van Heijningen, Visser, Zuidema, & ten Cate, 2009; Ravignani, Westphal-Fitch, Aust, Schlumpp, & Fitch, 2015). In those studies, a large amount of participants based their decisions on the detection of immediate repetitions within the former type of sequences, rather than on the processing of the full underlying grammars. Taken together, these studies and ours suggest that processing of complex grammars might be demonstrated in future studies with nonhuman species, if the test design avoids the presentation of adjacent repetitions within the sequences, to promote extraction of less salient regularities.

One limitation of our study is that the exact structure that the baboons have extracted remains uncertain. For instance in Experiment 1, baboons may have learned that the first and last elements are identical in the ABA patterns, without processing the fact that second element differs. Addressing this issue would also require additional experiments, contrasting for instance ABA against AAA sequences. Another limitation is that baboons were tested on visual pattern learning only. Whether the current findings would hold with auditory sequences remains unknown. Past studies with humans have revealed that sequential regularities extraction is highly constrained by several modality-specific and stimulus-specific features (for a review, Frost, Armstrong, Siegelman, & Christiansen, 2015). Studying those constraints in a comparative perspective will be mandatory to better understand the evolution of pattern learning abilities (Milne, Wilson, & Christiansen, 2018; Neiworth et al., 2017; Santolin & Saffran, 2018).

Baboons' results in the current study are in line with previous comparative researches suggesting that the ability to extract structural properties beyond exemplars is widespread among animal species. However, future studies may reveal differences between humans and other species, notably regarding the type of elements over which structural regularities can be extracted. In the current study, patterns are based on identity relationships at the token level (i.e., "A" being an arbitrary element which is repeated). However, in human language, structural regularities can also be found over *functional* categories (ten Cate & Okanoya, 2012; Corballis, 2009) and it remains unknown if nonhuman species have the capacity of extracting such language-like patterns. In addition, results from a recent neuroimaging study suggest that brain areas involved in sequential patterns encoding partly differ between humans and monkeys, possibly reflecting interspecific differences in the way the different features of a pattern are encoded (Wang, Uhrig, Jarraya, & Dehaene, 2015).

The nature of the mechanisms underlying the processing of the structural properties of sequences is a matter of a longstanding and still ongoing debate. Marcus et al. (1999; see also Marcus, 2001) argued that generalization to novel isomorphic sequences involves rulegoverned mechanisms and symbolic representations of the patterns. However, numerous alternative accounts were proposed for this behavior (e.g., Altmann, 2002; Altmann & Dienes, 1999; Brooks & Vokey, 1991; Christiansen & Curtin, 1999; McClelland & Plaut, 1999; Negishi, 1999; Pothos, 2005; Seidenberg & Elman, 1999). Most of these accounts argue that statistical learning mechanisms can explain generalization in these tasks, and do not postulate the existence of rule-based mechanisms. In a complementary perspective, Brooks and Vokey (1991) proposed that the subjects may compare the novel exemplars to a set of memorized exemplars, instead of comparing them to an abstract, symbolic, representation of these sequences’ structure. Although such alternative accounts are still debated (for a discussion, see e.g., Endress et al., 2007), they may ultimately offer a more parsimonious explanation of generalization in pattern learning studies, than the hypothesis of rule learning. As a third alternative, Endress, Nespor, and Mehler (2009) proposed that repetitions detection is supported by a specialized mechanism, belonging to a set of « perceptive and memory primitives ». These mechanisms are hypothesized to be automatic, would require little or no exposure to the stimuli to be recruited, and would take place in early stages of processing (Endress, Dehaene-Lambertz, & Mehler, 2007; Gervain et al., 2008). Endress, Carden, Versace, and Hauser (2010) proposed that some of these perceptual and memory primitives may be neither language- nor human-specific. Results from our second experiment are consistent with this last hypothesis, as baboons demonstrated a strong sensitivity to adjacent repetitions. However, this effect was not observed for non-adjacent repetitions, which suggests that if such mechanism exists, it is highly limited by memory constraints.

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