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IMPLICIT SEQUENCE LEARNING IN RING-TAILED LEMURS (LEMUR CATTA)

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Implicit learning involves picking up information from the environment without explicit instruction or conscious awareness of the learning process. In nonhuman animals, conscious awareness is impossible to assess, so we define implicit learning as occurring when animals acquire information beyond what is required for successful task performance. While implicit learning has been documented in some nonhuman species, it has not been explored in prosimian primates. Here we ask whether ring-tailed lemurs (*Lemur catta*) learn sequential information implicitly. We tested lemurs in a modified version of the serial reaction time task on a touch screen computer. Lemurs were required to respond to any picture within a 2×2 grid of pictures immediately after its surrounding border flickered. Over 20 training sessions, both the locations and the identities of the images remained constant and response times gradually decreased. Subsequently, the locations and/or the identities of the images were disrupted. Response times indicated that the lemurs had learned the physical location sequence required in original training but did not learn the identity of the images. Our results reveal that ring-tailed lemurs can implicitly learn spatial sequences, and raise questions about which scenarios and evolutionary pressures give rise to perceptual versus motor-implicit sequence learning.

Key words: implicit learning, sequence learning, ordinal reasoning, serial reaction time task, ring-tailed lemurs

Dialing a phone number, riding a bike, tying a shoe, and speaking a language are among the many sequential behaviors we learn to perform. Learning such activities often occurs outside of our conscious awareness and without the need for explicit instruction. For instance, as young children, we acquire grammatical rules of the language to which we are regularly exposed. Picking up information from a complex environment without conscious awareness of what was learned or perhaps even that learning has occurred is known as implicit learning (Cleeremans, Destrebecqz, & Boyer, 1998; Janacsek & Nemeth, 2012). Implicit learning contrasts with explicit learning, a process of hypothesis-testing (Abrahamse, deliberate Jiménez, Verwey, & Clegg, 2010). Implicit sequence learning is crucial for social interactions (Heerey & Velani, 2010; Lieberman, 2000), language acquisition (Conway, Bauernschmidt, Huang, & Pisoni, 2010; Granena, 2013), music appreciation (Ettlinger,

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Margulis, & Wong, 2011), and motor skills (Corkin, 1968), and may play a role in general intelligence and personality (Kaufman et al., 2010). Thus, over the past several decades, research into the varieties and mechanisms of implicit learning has flourished in humans. However, relatively little attention has been paid to what sorts of information other animals are capable of learning implicitly.

In nonhuman animals, implicit learning is difficult to disentangle from explicit learning because there are no behavioral markers of consciousness in other species. Thus, conscious awareness of what was learned cannot be assessed. In fact, animal studies typically do not specify whether any evident learning was implicit or explicit.

An important exception is the study of episodic memory, a form of explicit learning. For example, research with scrub jays (*Aphelocoma coerulscens*) demonstrates memory for what, when, and where they have cached different food items (Clayton & Dickinson, 1998), as well as which caches they have visited previously (Clayton & Dickinson, 1999). Even here, though, the impossibility of attributing consciousness to the birds' recall of past events prevents their behavior from fulfilling the definition of episodic memory in humans (Griffiths, Dickinson, & Clayton, 1999).

Therefore we operationally define implicit learning in animals as any learning that occurs when animals acquire information beyond what is required for successful task performance. Explicit learning, on the other hand, would involve learning that is necessary for successful task performance, such as when subjects must learn to respond to a particular stimulus or feature to obtain reward.

A common paradigm for assessing implicit learning in humans is the serial reaction time task (SRTT). In the original SRTT, an asterisk symbol was presented in one of four places on a monitor, and subjects were required to press the key on a keyboard that was directly below the symbol (Nissen & Bullemer, 1987). When the sequence of four symbol positions repeated, subjects' reaction time sharply decreased over the course of the experiment; but, when the symbol randomly appeared in different positions, reaction times did not show this dramatic decline. The percentage of correct choices also increased moderately in the repeating condition, but not in the random condition. These accuracy and reaction time measures both suggest that subjects learned the repeating sequence, despite the fact that the task did not require learning the sequence.

Versions of the SRTT have been used to explore implicit sequence learning in rodents, birds, and monkeys. For example, mice (Christie & Hersch, 2004) and rats (Christie Dalrymple-Alford, 2004; Domenger & & Schwarting, 2005) that were trained to nosepoke one of four holes according to a cue light performed more efficiently when the lights appeared in a repeating sequence rather than randomly. Pigeons (Columba livia) pecking at keys cued in a repeating sequence exhibited higher response times when a key was cued outof-sequence (Helduser & Güntürkün, 2012) (see also Locurto, Fox, & Mazzella, 2015). Rhesus macaques (Macaca mulatta) touching lit targets on a computer monitor responded more slowly when targets were cued in a random rather than a fixed sequence (Lee & Quessy, 2003; Procyk, Ford Dominey, Amiez, & Joseph, 2000). Similarly, when rhesus macaques were trained to use a joystick to respond to targets presented on a computer monitor, response times were faster for sequences that repeated compared to novel or randomized sequences

(Heimbauer, Conway, Christiansen, Beran, & Owren, 2011; Turner, McCairn, Simmons, & Bar-Gad, 2005). Finally, Locurto and colleagues have performed several studies using the SRTT with cotton-top tamarin monkeys (Saguinus *oedipus*) in which subjects touched a picture appearing in one of several locations on a touch-screen. Tamarin monkeys responded more slowly during random than repeating sequences across various reinforcement schedules and regardless of whether the sequence was defined based on the identity of the visual images or spatially based on the required motor responses (Locurto et al., 2015; Locurto, Dillon, Collins, Conway, & Cunningham, 2013: Locurto, Gagne, & Levesque, 2009; Locurto, Gagne, & Nutile, 2010).

An unresolved question in the human SRTT literature is the degree to which perceptual relative to motor implicit sequence learning occurs. When people are required to follow a particular sequence, do they encode the physical responses required (i.e. the fifth, followed by the first, followed by the fourth position in a line) or the identity of the items (i.e., the letter B, followed by the letter X, followed by the letter G), or perhaps both to differing extents? Some studies have suggested that implicit sequence learning is primarily based on motor responses (e.g., Verwey & Clegg, 2005; Willingham, 1999), others have found that learning can be specific to the perceptual stimuli (e.g., Clegg, 2005; Howard, Dennis, Howard, Yankovich, & Vaidya, 2004), and still others have found evidence for both types of learning within the same task (e.g., Deroost & Soetens, 2006; Gheysen, Gevers, Schutter, Waelvelde, & Fias, 2009). This question has only been addressed in one nonhuman animal, cotton-top tamarins. In this case, the monkeys seemed to learn both types of information equally (Locurto et al., 2010).

Here, we ask whether a prosimian primate, the ring-tailed lemur (*Lemur catta*), exhibits implicit sequence learning. Prior work has shown that ring-tailed lemurs can learn ordered information explicitly, when sequence knowledge is required for reinforcement (Merritt, MacLean, Jaffe, & Brannon, 2007), and that they can reason transitively about elements in an ordered list (Maclean, Merritt, & Brannon, 2008). A second question this research asks is whether lemurs are more apt to encode the sequence based on identity information, spatial information, or a combination of the two.

We used a touch-screen version of the SRTT in which four images were presented simultaneously on the screen, and subjects simply had to touch the image with a flickering border. During training, the four images always appeared in the same location and the order in which they had to be touched repeated in a predictable pattern. For example, the sequence might be picture A in location 4, followed by picture B in location 1, followed by picture C in location 3, followed by picture D in location 2, and repeat. In three different testing conditions, the spatial sequence, the picture identity sequence, or both the spatial and picture identity sequences were changed. If lemurs learned the spatial (or identity) aspect of the training sequence, then they should respond more slowly and/or make more errors during testing when the spatial (or identity, respectively) sequence was disrupted.

Method

Subjects

Four adult ring-tailed lemurs (*Lemur catta*), three male (Berisades: 9 years old, Licinius: 20 years old, and Teres: 18 years old) and one female (Sierra Mist: 5 years old), pair-housed in indoor/outdoor enclosures at the Duke Lemur Center were tested. Licinius and Teres had extensive prior touch-screen experience in numerical and ordinal tasks; Berisades participated in one previous numerical touch-screen study; and Sierra Mist had not previously used a touch-screen. Subjects had unrestricted access to water and were fed normally throughout this study. All procedures reported here were approved by the Duke Institutional Animal Care and Use Committee.

Apparatus

During testing, the subject animal was separated from his or her cage mate, and a portable stainless-steel testing station (62cm X 62cm X 33cm) housing all experimental material was placed in the subject's home enclosure (see Fig. 1). Stimuli were presented on a 12-inch touch-sensitive computer monitor (Elo TouchSystems, Menlo Park, CA). A food pellet reward delivery system (Med Associates, St. Albans, VT) was used to deliver 190-mg sucrose pellets (TestDiet, St. Louis, MO) below the screen. Plexiglas templates with holes for the stimuli were placed over the monitor. A plastic box was placed in front of the screen for the lemurs to sit on in order to reach the screen. Stimulus presentation, reward delivery, data collection, and data analysis were performed via custom-written programs in MATLAB (Mathworks, Natick, MA) with the Psychophysics Toolbox add-on (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007) (https://psychtoolbox. org).

Procedure

Stimulus selection training. The goal of this phase of training was to instruct the lemurs to touch a stimulus with a flickering border. On each trial, two colored rectangles appeared in any of nine locations (comprising a 3×3 array) on the screen over a gray background, and an 8- mm black-and-white border flickered (i.e., the black and white areas swapped places) around one of them. The trial ended when the lemur touched the rectangle with the flickering



Fig. 1. Experimental task. A ring-tailed lemur sits in front of a touch screen and presses the one of four images with a flickering black-and-white border. After a subset of correct presses, a pellet reward is delivered out of the apparatus near the lemur's left foot in this photograph.

border, and the next trial began after an intertrial interval of 0.3s for correct trials and 1.5s for incorrect trials. Accuracy was the percentage of trials on which the lemur first touched the stimulus with the flickering border. The trial did not end until the lemur touched the rectangle with the blinking border. Upon touching the correct rectangle, a positive tone played and a reward was delivered probabilistically. Reinforcement began at 100%, and was reduced to 75%, 50%, and 25% after two sequential sessions with median response times (RTs) under 2.5s and accuracies of at least 90%, or accuracies of at least 85% (or 80%) if the subject had already completed 10 (or 20, respectively) sessions at the same reinforcement level. Each session was terminated when the lemur received 50 pellets and consisted of between 50 and 200 trials. Subjects continued to the next training phase after completing three sequential sessions at 25% reinforcement with median RTs (excluding trials after receiving a pellet) under 2.5s and accuracies of at least 85%.

Implicit sequence training. The goal of the next phase of training was to have the lemurs implicitly learn a four-response sequence. Four pictures (comprising a 2×2 array) were presented on the screen. The black-and-white flickering border appeared around each of the four pictures in a predictable sequence. The sequence was predictable based on both the order of the images (e.g., bird, flower, ocean, monkey) and the spatial locations (e.g., top right, bottom left, top left, bottom right). After the first blinking stimulus was touched, the border disappeared and immediately began flickering around the second stimulus, and so forth. Each time the lemur touched the stimulus with the flickering border, a positive tone played, and a reward was delivered on a pseudorandomly-selected 25% of trials (under the constraint that reward followed a touch to each stimulus an equal number of times). The border flickered around the four stimuli in a four-item repeating sequence, i.e. ABCDABCD. Crucially, lemurs were not required to learn this sequence in order to obtain reward, but only to touch the stimulus with the flickering border, as in stimulus selection training. The four locations and images used were the same for all subjects, but the spatial and identity sequences during training followed two different patterns, with Licinius and Sierra Mist receiving one

pattern, and Berisades and Teres receiving the other. Each session consisted of 200 trials (one trial is one correct touch to a stimulus), equivalent to 50 repetitions of the four-item sequence. Subjects initially completed either 30 sessions of implicit sequence training, or at least 20 sessions if their median RT (excluding trials after a reward, and the session's first trial) fell below 1 s in their last session.

Testing. The procedure during testing was the same as in implicit sequence training: Four pictures appeared onscreen and the lemur had to touch the stimulus with a flickering border. The predictable sequence used in the previous phase of training was disrupted in three different ways to determine what the lemurs had learned in the implicit training phase. In the Spatial-Novel condition, the image pattern remained the same as in training, but the required motor pattern was novel. In the Identity-Novel condition, the spatial pattern remained the same as in training, but the image pattern was novel. In the Both-Novel condition, both the spatial pattern and the image pattern were disrupted. Subjects completed two testing sessions in each condition. In between testing conditions, subjects completed another five sessions of implicit sequence training to re-familiarize them with the baseline sequence. All subjects completed Both-Novel testing first, and the orders of Spatial- and Identity-Novel testing were counterbalanced across subjects: Berisades and Sierra Mist completed Spatial-Novel testing before Identity-Novel testing, whereas Licinius and Teres completed Identity-Novel testing before Spatial-Novel testing.

Data analysis. First, we examined whether response time (RT) decreased over implicit sequence training by creating a generalized linear regression model (GLM) with predictors subject and session number, and their interaction. We excluded the RT to the first trial and any trial after reward delivery. We further excluded any trial for which RT was greater than two standard deviations above the mean RT for each subject (3.52% of trials for Berisades, 1.67% for Licinius, 0.56% for Teres, and 3.02% for Sierra Mist). Finally, we normalized the RT data by subtracting the mean RT of the remaining trials for each subject from that subject's RTs.

To assess whether the lemurs had learned the identity or spatial sequence, we compared RTs in the training and test conditions. We compared mean normalized RT for each test condition to the mean RT for the last two training sessions prior to that test condition for each subject. We ran a 4 (subject) X 6 (condition) ANOVA on RT, where the six conditions were the three testing conditions and the three training blocks prior to each condition. We considered the training blocks separately in the ANOVA to account for order effects (e.g., the subject may have become faster at responding as the experiment proceeded). Additionally, we ran similar ANOVAs using only the first 10, 25, 50, and 100 trials of the final training and first testing sessions in each condition, as well as the full 200-trial final training and first testing sessions (rather than the two final training and two testing sessions) in each condition. To further examine differences in RT among testing conditions, we created a GLM predicting normalized RT from testing condition (spatial, identity, both, or neither [i.e., training]) and subject. Finally, we defined an error as a trial in which the subject touched a stimulus that was not flickering prior to ultimately touching the stimulus with the flickering border. We ran chi-square tests to assess whether error ratesthat is, choice accuracy-differed among the conditions.

Results

Over the course of the 20 implicit sequence training sessions, subjects' response times significantly decreased (overall difference from constant model: $F_{12022}=37$, p < .0001; coefficient for session: $\beta = -0.0430$, t = -13.85, p < .0001). This decrease suggests that subjects learned the sequence, although it could also reflect increasing facility with the general task demands.

Subjects' sequence learning was confirmed by an increase in RT during testing (Fig. 2). An ANOVA revealed a significant main effect of condition ($F_5 = 28.24$, p < .0001), no main effect of subject ($F_3 = 0.00017$, p = 1), but a significant condition-by-subject interaction ($F_{15} = 2.718$, p = .00036). Tukey-Kramer posthoc tests revealed that the differences between Both-Novel testing and the immediately preceding training block (M = 0.153s, CI =[0.0837, 0.2226], p < .0001), and between Spatial-Novel testing and the immediately preceding training block (M = 0.1955s, CI =



Fig. 2. Response time across conditions. The three different testing conditions are indicated on the x-axis. The mean normalized RT in each testing condition is shown in dark gray, and the mean normalized RT in the training block preceding each testing condition is shown in light gray. Error bars represent standard error of the mean. The differences between Both-Novel testing and training, and between Spatial-Novel testing and training, were significant, whereas the difference between Identity-Novel testing and training was not (see text for statistics).

[0.1264, 0.2646], p < .0001), were significant, whereas the difference between Identity-Novel testing and the immediately preceding training block was not significant (M = 0.0407s, CI = [-0.281, 0.1096], p = .5415). All individual subjects (Fig. 3) performed more slowly in Both-Novel testing than in the immediately preceding training block (significant at p < .05only for Sierra Mist) and in Spatial-Novel testing than in the training block immediately before it (significant at p < .05 for Berisades, Teres, and Sierra Mist). Berisades, Teres, and Sierra Mist showed small but nonsignificant increases in RT in Identity-Novel testing compared to the immediately preceding training block, whereas the reverse pattern was exhibited by Licinius (all ps > .1).

If the effects of spatial and identity sequence disruption were additive, then we should expect RTs to be significantly greater for Both-Novel compared to Spatial-Novel. To test this prediction, we ran a GLM predicting normalized RT from the binary factors Image-Novel (1 in Image- and Both-Novel testing, 0 in training and Spatial-Novel testing), Spatial-Novel (1 in Spatial- and Both-Novel testing, 0 in training and Image-Novel testing), and their interaction, as well as subject. The overall model was significantly different from the constant model ($F_{7004} = 22.6$, p < .0001). The only significant coefficient was for Spatial-Novel ($\beta = 0.1777$,



Fig. 3. Raw response time across conditions for each individual subject. The two subjects in the top row (Berisades and Sierra Mist) received Identity-Novel testing before Spatial-Novel testing. The two subjects in the bottom row (Licinius and Teres) received Spatial-Novel testing before Identity-Novel testing. The three different testing conditions are indicated on the x-axes. The mean RT in each testing condition is shown in dark gray, and the mean RT in the training block preceding each testing condition is shown in light gray. Error bars represent standard error of the mean.

t=8.942, p<.0001; all other ps>.1). This pattern of results indicates that the increase in RT during Both-Novel testing could be attributed entirely to the change in the spatial sequence, with no contribution from the change in the identity sequence.

To address the possibility that the effects of sequence disruption—particularly those of the visual sequence—may have quickly washed out over the course of testing, we performed additional tests including only the first testing session in each condition, and the final training session before it. We ran five ANOVAs using the first 10, 25, 50, or 100 trials from each of these sessions, or the full 200-trial sessions. We included the same number of trials from the beginning of the final training sessions in order to control for any possible changes in behavior over the course of each session.

When only 10 trials from each session were included, there was no main effect of condition ($F_5 = 1.83$, p = .11) nor a condition by subject interaction ($F_{15} = 1.21$, p = .27). When 25 trials

were included, there was a significant main effect of condition ($F_5 = 3.82$, p = .0022) and no condition by subject interaction ($F_{15} = 1.05$, p=.40). Post-hoc Tukey-Kramer tests revealed that the difference between spatial-novel testing (M = 0.297s, CI = [0.222, 0.372]) and the training preceding it (M = -0.080s, CI =[-0.155, -0.0054]) was significant with p < .05, but the differences between both-novel testing (M = 0.159s, CI = [0.084, 0.235]) and the training preceding it (M = -0.076s, CI =[-0.150, -0.001]), and identity-novel testing (M = 0.017s, CI = [-0.058, 0.092]) and the training preceding it (M = 0.028s, CI =[-0.046, 0.102]) were not. This same pattern of effects by condition held when 50 or 100 trials were included (although there were also significant condition by subject interactions); that is, the difference between Spatial-Novel testing and the training before it was significant, but the differences between Identity-Novel and Both-Novel testing and the training sessions before them were not significant at the

p < .05 level. When all 200 trials from each session were included, there was again a main effect of condition ($F_5 = 17.55$, p < .0001) and a condition by subject interaction ($F_{15} = 1.72$, p=.027). Now, post-hoc Tukey-Kramer tests revealed significant differences at p < .05between Both-Novel testing (M = 0.062s, CI =[0.038, 0.085]) and the training before it (M = -0.054s, CI = [-0.077, -0.030]), as well as between Spatial-Novel testing (M = 0.150s,CI = [0.127, 0.174]) and the training before it (M = -0.112s, CI = [-0.136, -0.089]), but still no significant difference between Identity-(M = 0.010s, CI = [-0.013,]Novel testing (0.034]) and the training before it (M = -0.081s, CI = [-0.105, -0.058]). Thus, we find no evidence that changing the identity sequence altered lemurs' behavior, even at the very beginning of testing.

To complement the RT analyses, we next examined error rates. A chi-square test indicated that there were significant differences in error rates across conditions ($\chi^2 = 30.18$, p < .0001). Follow-up chi-square tests comparing each testing condition to the immediately preceding training block, and using a Bonferroni-corrected threshold *p*-value of .05/3 =.0167, revealed that subjects made significantly more errors during Spatial-Novel testing (5.76%) than the immediately preceding training block (2.30%, $\chi^2 = 18.16$, p = .00002). The same analyses for the rates in Identity-Novel testing (2.71% vs. 3.15%, $\chi^2 = 0.3910$, p = .53), and Both-Novel testing (4.86% vs. 4.81%, $\chi^2 = 0.0037, p = .95$) were not significant.

Discussion

We examined whether ring-tailed lemurs spontaneously and implicitly encode spatial and identity sequences. Subjects were trained to touch stimuli with flickering borders and were presented with sequences of images with flickering borders that maintained a consistent spatial and identity order. After 20 sessions with a sequence that remained constant both in the order of the stimulus identity and spatial locations, all four lemurs' response times decreased substantially. We confirmed that the drop in lemurs' RT resulted from learning some aspect of the training sequence, rather than some other general factor like an increased facility with the touch screen task, by testing them with novel sequences that

disrupted both the spatial and identity information in the original sequence. In this case, response time significantly increased. This finding suggests that lemurs encoded the motor sequence required, the order of the pictures themselves, or both types of information to some degree.

We then asked whether lemurs found spatial or identity information to be more salient. We found that changing only the order of the pictures themselves while keeping the spatial sequence constant did not significantly affect RT; however, the reverse did significantly impact RT. This result held even when we considered only the early testing trials. Additional analyses suggested that changing both spatial and identity components of the sequence did not result in additive impacts on RT. Together, these results suggest that lemurs learned the spatial sequence, but not the identity of each image in the sequence. Although identity information was an available cue for the lemurs, it seems that the flashing border and the spatial information overshadowed it.

Our finding that lemurs learned the spatial, but not the identity information in a repeating sequence stands in contrast to the findings of Locurto and colleagues (2010) in cotton-top tamarins. These monkeys acquired both motor and perceptual sequential information. Although it is possible that this is a true difference between ring-tail lemurs and tamarin monkeys, it is equally possible that the different patterns of results stem from methodological differences.

For instance, we did not include any intertrial interval between stimuli or between repetitions of the sequence, whereas tamarin monkeys received a 5-s white screen prior to the first element in a chain and a 20-second black screen following the final element (Locurto et al., 2009, 2010, & Experiment 1 of 2013), or a 1-s ITI between every pair of elements (Locurto et al., 2013, Experiment 2). It could be that forcing subjects to pause between responses encouraged perceptual encoding of the responses. Also, for tamarins, images appeared one-at-a-time onscreen, whereas in our study all four images remained onscreen the entire time. Although it might be expected that the consistent exposure in our study could lead to greater encoding of the visual array, it is also possible that the sudden appearance of each item in Locurto et al. (2010) caused subjects to pay more attention to its identity. Moreover, because our stimuli remained onscreen, lemurs could have very quickly become accustomed to the new visual arrangement. In addition, for the tamarins, visual learning was initially tested following visual-only training: That is, during training, the images appeared in random locations on the screen, so there was no repeating motor pattern (Locurto et al., 2009, and Experiment 1 of Locurto et al., 2010). It is possible that if lemurs were trained in this way, then they would also show sensitivity to the image identity. Finally, tamarins in Experiment 2 of Locurto et al. (2010) which were trained with the same image appearing in a repeating spatial pattern not only showed evidence of motor learning, but also of visual learning; their reaction times increased during "Wild Card" testing when a novel image was displayed. It is possible that if we had introduced entirely novel images during Visual-Only Testing, rather than a reordering of the same four images used in training, then lemurs' response times would have increased. Further experiments more closely mirroring the procedures of Locurto and colleagues (2010) would help determine whether there are species differences in the implicit sequence learning tendencies of lemurs and tamarins.

It is of course possible that future research using different parameters may reveal that lemurs can implicitly encode identity information. In addition to the possibilities discussed in the previous paragraph, it could be that the images used in this study were not salient enough for ring-tailed lemurs to effectively discriminate them. However, the images are similar to those used in other studies from our group where reward was contingent upon discriminating identity information (e.g., Merritt et al., 2007). It is also notable that rhesus monkeys (Kornell & Terrace, 2007) and pigeons (Staniland, Colombo, & Scarf, 2015) failed to encode visual sequential information when tested in a sequence-learning task where a "hint" in the form of a border around the correct image was present.

Another reason that spatial, but not visual learning may have occurred in our study is that spatial learning could have facilitated the motor speed of task performance, thereby bringing subjects closer to reinforcement. It is less clear how visual learning would have enabled faster movements and thus produced an earlier reward. Using a different task paradigm, in which visual learning would be beneficial to the subject, might reveal this form of implicit learning.

It should also be noted that Both-Novel testing always occurred before either Visual-Novel or Spatial-Novel testing. Although we included five additional sessions of implicit sequence training between testing conditions, it is possible that exposure to the Both-Novel condition altered behavior in the subsequent testing conditions, and an effect might have been observed in the Visual-Novel condition had it been run first. This issue is relevant to the controversy in the human literature over the predominance of motor versus perceptual implicit learning. Understanding how these two types of learning evolved could shed light on which situations should favor the use of motor or perceptual cues, and on whether implicit sequence learning involves shared or entirely distinct cognitive structures for motor and perceptual sequences.

The experiment reported here did not attempt to dissociate spatial learning at the stimulus stage from motor learning at the response stage. The physical location on the screen where the flickering border appeared was always the same as the response location the subjects needed to touch. The increase in RTs in the Spatial- and Both-Novel tests could be explained by the lemurs encoding the spatial location of either the stimulus or the response. The former case would be an example of perceptual learning. Whether stimulus-based or response-based learning predominates in human implicit sequence learning has been a contentious issue, with task conditions being a likely determinant of which type of learning occurs (Abrahamse et al., 2010). Additional studies are needed to tease apart whether lemurs' learning of the location sequence relied on perceptual spatial learning or motor response learning.

Another avenue for future research would be a comparison of implicit sequence learning abilities across different lemur species. Ringtailed lemurs have been shown to possess sophisticated ordinal reasoning abilities (Merritt et al., 2007), outperforming other lemur species in certain tasks (Maclean et al., 2008). In light of these species differences in explicit sequence learning, it would be interesting to examine whether other lemurs implicitly learn sequences. can Because other animals including rodents (Christie & Dalrymple-Alford, 2004; Christie & Hersch, 2004; Domenger & Schwarting, 2005) and birds (Helduser & Güntürkün, 2012; Locurto et al., 2015) are able to implicitly acquire sequences, we expect that other lemurs would be able to do so as well, but the speed and degree of learning may vary across species. Such a comparison might lend insight into the evolutionary pressures favoring the capacity for implicit learning. For instance, if ring-tailed lemurs outperform other species that live in smaller social groups, then implicit sequence learning may have evolved alongside explicit sequence learning to support complex social structures. Alternatively, if other lemur species are equally capable of implicit sequence learning, then it may be a fundamental skill necessary for survival in a variety of ecological niches.

A final important caveat is that our study did not actually attempt to differentiate between types of learning. We defined implicit learning as encoding of information that was not necessary for successful task performance. By this definition, we argue that any learning of spatial or identity sequence information was implicit. However, we did not assess potential explicit knowledge of the sequence. Regardless, our study demonstrates that ring-tailed lemurs encode a spatial sequence even when knowledge of this sequence is not required for reinforcement in the task. Our study further suggests that lemurs are less inclined to encode a sequence based on visual identity cues. To our knowledge, this study is the first demonstration of implicit learning in a prosimian primate. It opens the door for comparative studies of implicit learning across ecologically diverse lemur species.

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