

Implicit Chaining in Cotton-Top Tamarins (*Saguinus oedipus*)

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In implicit learning, human subjects are exposed to patterned information, but they are not informed about the pattern. Typically, they demonstrate learning of that pattern, but little awareness of the experimental contingencies. In a nonhuman analog of this procedure, two cotton-top tamarins (*Saguinus oedipus*) were presented with a five-element chain that consisted of the same icon presented serially at different locations on a touchscreen. The tamarins had to touch the icon at each location to advance the chain and receive reinforcement at the end of the chain. One element of the chain was never differentially reinforced in the presence of another element, as is typically done in transitive inference and serial chaining studies. Following training, the tamarins were tested for their knowledge of the chain using pairwise tests that are common in transitive inference and serial chaining experiments, and a random test, common in some types of implicit learning, in which the sequence of elements was randomized. The results of both tests revealed that the tamarins appreciated the ordinal position of the elements composing the chain, although reinforcement had not been dependent on that knowledge.

Keywords: implicit learning, serial learning, serial reaction time, tamarins

The study of serial learning has resulted in the identification of a number of parallels between humans and nonhumans (Terrace, 2001). These parallels include the finding that nonhumans can often master tasks that were originally developed in humans, such as transitive inference (Wynne, 1997), multiple list learning (Treichler & Van Tilburg, 1996), and simultaneous chains (Swartz, Chen, & Terrace, 1991). Serial learning in nonhumans also reflects characteristics of human performance, such as serial position effects (Wright, Santiago, Sands, Kendrick, & Cook, 1985) and the organization of sequential elements into chunks (Terrace, 2001). Not surprisingly, a number of lines of evidence indicate that the memorial and representational processes that underlie serial learning are common among humans and nonhumans (D'Amato, 1991).

In one respect, however, the study of serial learning in humans does not presently have a well-developed parallel in the nonhuman literature. The discrepancy concerns implicit learning, a form of learning in which the acquisition of patterned information is not typically accompanied by subjects' awareness of the experimental contingencies. Reber (1967) initiated the investigation of implicit learning by studying the acquisition of a set of letter strings that had been formed according to a finite state grammar. He observed that these strings were learned more readily than were strings that had been composed randomly with respect to that grammar, even though subjects were not told that there was an underlying grammar. Moreover, some but not all subjects were unable to articulate the rules of that grammar at the end of the experiment, hence, the name implicit for this type of learning.

There are numerous demonstrations that various forms of patterned information can be acquired implicitly in humans (Clegg, DiGirolamo, & Keele, 1998; Seger, 1994). One of the most investigated forms is the serial reaction time (SRT) task in which an icon is repeatedly presented on a computer screen, usually in one of four positions. Subjects are asked to tap a designated key that corresponds to the position of the icon. The icons is presented in a pattern, usually 8 to 12 elements in length, but subjects are not informed that icon presentations are patterned. The typical finding is that subjects' reaction times decrease substantially during training with the pattern, and rise during tests in which the icon is presented at randomly chosen locations. As is typical in other forms of implicit learning, in post-experimental assessments most but not all subjects demonstrate no awareness that a pattern governed icon presentation (Seger, 1994).

There are presently few adaptations of implicit learning procedures for nonhumans, although there are important exceptions in studies using nonhuman primates (Fitch & Hauser, 2004) and birds (Gentner, Fenn, Margoliash, & Nusbaum, 2006). Perhaps the most investigated adaptation comes from studies that have used the SRT task rather straightforwardly, absent the obvious inability to test for awareness following training. In these adaptations, subjects, usually rodents, are exposed to a serial pattern that involves four stimulus locations. Subjects are required to respond to each stimulus to advance the pattern to the next stimulus. Following training, a random test is used to observe whether latencies rise as they do in humans. These adaptations have yielded evidence of decreases in latencies during training on the pattern, and increases in latencies during a random test (e.g., Domenger & Schwarting, 2005). In these studies, the term implicit may be taken to mean that knowledge of the pattern is not needed to produce reinforcement. A subject can adopt a simple rule, such as "Nose poke any stimulus that lights up," that need not be based on patterned information, but could nonetheless result in the same reinforcement rate as that obtained by a subject who learned the pattern.

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One shortcoming of SRT tasks compared with other assays of serial learning is that the same location is used to display multiple elements in a pattern. For example, the upper-right quadrant of a computer screen may be the location for the second, eighth, and tenth elements in a 12-element pattern. It is, as a consequence, not possible to assess the value of individual elements in a pattern, as is routinely done in studies of transitive inference and chaining wherein elements of the pattern are unique, either spatially or visually.

The present study married the SRT procedure with design features taken from transitive inference and serial chaining studies. We presented cotton-top tamarins with a five-element serial chain. Each element of the chain occupied a unique spatial location on a touchscreen. Subject had to touch each icon to advance the chain to the next spatial location, but knowledge of the pattern was not necessary for reinforcement. Following a response to the fifth icon presentation, reinforcement was delivered. The tamarins' understanding of the pattern was assessed following training by pairwise tests between elements of the chain, as are common in transitive inference and chaining studies, and by a test in which elements of the pattern were presented randomly, as is common in SRT tasks.

A word about nomenclature: We have adopted the term implicit chaining for this procedure, rather than referring to it as a type of SRT task. There are presently two different tasks that are referred to as serial reaction time tasks, neither of which captures some of the unique features of our procedure, particularly the posttraining assays that are possible, and, as discussed later, procedural alterations that can be implemented to assess the nature of learning in this task. In addition to the SRT task described earlier, there is another procedure, in the animal literature, referred to as a serial reaction time task. In this second task, one of five nose pokes is illuminated serially, and the subject, rat or mouse, must respond to each nose poke to obtain reinforcement. There is no pattern to the stimulus presentations, and there are no assessments of what has been learned following training. The task is a type of vigilance or sustained attention assay that has proven sensitive to a number of pharmacological interventions (see Robbins, 2002, for a review).

Method

Subjects

Two male cotton-top tamarins (*Saguinus oedipus*) served as subjects. They were housed individually at the New England Regional Primate Research Center, Southborough, Massachusetts. One subject, Windsor, was 19 years old at the start of training; the second subject, Winston, was 14 years old. The average age of members of the colony was 7.5 years. Both tamarins were among the approximately 19% of the colony that was more than one standard deviation above the average colony age. Neither animal had previously participated in any research project, both had been born at the center and had been housed there throughout their lives. Subjects were maintained in accordance with the guidelines of the Committee on Animals of the Harvard Medical School. Their daily feeding regimen consisted of two feedings, one in the morning, the second in the afternoon. Feedings consisted of monkey chow supplemented with fresh fruit. On training days they received their morning feeding for approximately two hours. Food was removed three hours prior to training. They received their afternoon feeding

immediately following a session. With this schedule, each subject was maintained at about 95% of their free-feeding weight at the time of training. Training was conducted on average four times each week.

Apparatus

The training stimulus consisted of the image of a sliced orange (approximately 200×200 pixels) presented on a touchscreen (ELO CarrollTouch infrared touchscreen, 38.1 cm on the diagonal; Tyco Electronics, Berwyn, PA). The front of the touchscreen was fitted with a clear Plexiglas bezel that allowed access to the touchscreen at six locations (10×10 cm holes cut out of the bezel) arranged in a 2×3 array across the touchscreen. The image was always displayed in the middle of one of the five locations used in this experiment. The bezel was used to prevent the tamarins from swiping their hand across the screen, thereby producing a number of touches during a stimulus presentation, a behavior that had been observed during pilot training. Reinforcement consisted of two 45-mg chocolate sucrose pellets (Test Diet, Purina Mills, LLC) delivered via a rotary pellet feeder (Coulbourn Instruments, Allentown, PA) into a dish located directly in front of the bottom left side of the touchscreen.

Subjects were tested in their home cage. We followed this procedure because pilot training had indicated that these animals exhibited high levels of agitation and avoidance when we tried to remove them from their cages. This procedure has precedent in other work that has identified several advantages in allowing primates to remain in their home cage during training (e.g., Crofts et al., 1999). The touchscreen was placed in front of the subject's home cage by using a load lifter (Genie Industries, Redmond, WA). The front door to the animal's cage was then opened, allowing the subject access to the touchscreen and reinforcement dish.

Procedure

Shaping. Training began with an autoshaping procedure in which the image was presented for 6 sec in the same location on each trial, upper center of the touchscreen, and was followed by food. If the subject touched the image during this time, the image was removed from the screen and food was immediately presented. If no response occurred, food was presented at the end of 6 sec. Sessions consisted of 40 trials. This procedure was continued until a touch response occurred to the image on 80% of the trials in a session for two consecutive sessions, and all reinforcers had been consumed in each session. For Windsor this procedure lasted for eight sessions; for Winston, nine sessions. In the second phase of training, the image was moved to different locations on the touchscreen, and remained there until a response terminated the trial and produced food. This phase lasted until responding occurred on each trial of the 40 trial sessions for two consecutive sessions. Sessions terminated after one hour if the subject did not complete the 40 trials. For Windsor, that criterion was reached in 10 sessions; for Winston the criterion was reached in 11 sessions. Following completion of this phase, training began on the five-item chain.

Acquisition. Acquisition consisted of one 40-trial session each day. Each trial consisted of the serial presentation of the image in the five different spatial positions on the touchscreen. These po-

sitions will hereafter be referred to as elements A (bottom right), B (top center), C (top left), D (bottom center), and E (top right), to indicate serial position in the chain. A response to the image at one position moved it to the next position without delay. Food followed a response to the image at position E. Five of the six possible spatial positions were used; the lower left position, directly behind the food dish, was not used. Trials were separated by a 20-sec intertrial interval (ITI) in which the touchscreen was dark. As a ready signal, before each trial the screen was illuminated and remained blank for 5 sec prior to the presentation of the first image of the chain.

Acquisition continued until a criterion was met that at least 15 40-trial sessions had been completed, and the total session time for each of the last three sessions was within $\pm 10\%$ of the mean for those three sessions. Total session time was used as the acquisition criterion because in this procedure there are no correct or incorrect responses, and hence, no performance criteria involving errors. As the ITI and ready signal were fixed throughout a session, variability in session time was due to differences in latencies to respond to the elements of the chain. For Windsor, meeting this criterion required 18 sessions; Winston met the criterion after 15 sessions. This amount of training, between 600 and 720 trials prior to testing (40 trials \times 15 or 18 sessions), corresponds to the amount of training that is found in a number of human serial reaction time studies (e.g., Rowland & Shanks, 2006; 1,000 trials), although there are numerous studies that involve considerably more training (e.g., Hunt & Aslin, 2001; 3,360 trials).

Testing: Pair-wise tests. Following acquisition, two types of tests were conducted. The first test consisted of pairwise presentations of stimuli to determine stimulus preferences. Testing began with the training of two pairs that were of particular interest based on prior work in transitive inference and chaining, the internal pair B/D, and the comparison of the end elements, A/E (e.g., Dusek & Eichenbaum, 1997). In testing these pairs, each test session consisted of 40 trials. The first 10 trials consisted of the serial presentation of the chain A – E followed by food, as had been done in acquisition. All chain trials were conducted in this manner during testing. Among the next 30 trials, 10 were pairwise tests and 20 were chains. The pairwise tests were interspersed among the chains such that two pairwise tests were separated by at least one chain. In all pairwise tests, reinforcement followed the first response to either element. That first response terminated the trial. Testing began with sessions in which only the B/D pair was tested. Windsor received eight sessions of this test. Winston received three sessions. The extended testing of Windsor, who was the first tamarin tested, was conducted to see whether preference changed as a function of extended training. Following testing of B/D, the A/E pair was tested. Windsor received four sessions of this pair test; Winston received two sessions.

For the final 10 sessions, both tamarins were tested on the remaining eight possible pairs. Each of these pairs was presented twice each session. During these sessions, the first 5 trials were chains. Among the next 35 trials, 16 were pair tests, and 19 were chains. Trials were arranged such that no two pairwise tests occurred consecutively. For purposes of analysis, the first 20 presentations of each pair were used.

Testing: Random sequences. The second test, conducted during the last session, consisted of the presentation of random sequences. Following 20 chains, 20 randomized chains were pre-

sented. Each random chain ended with reinforcement. Randomization was accomplished with two restrictions: on any trial a stimulus could occur only once; and, each stimulus occurred four times in each serial position during the test. In addition, we equated the randomized chains with the chains used in acquisition in terms of the total distance between the five elements of the chain. Counting adjacent spatial locations as 1 unit apart, and further locations as 2 or 3 (maximum) units apart, the training chains had a total distance of 7.0 units, whereas random trials averaged 6.65 units ($p > .05$, Mann-Whitney U test). For the random chains, of the possible 80 transitions between elements (e.g., A \rightarrow B, etc., 4 transitions per chain, 80 in 20 trials), 14 were the same as those occurring during training.

For all latency analyses during the random test, in which there was only a single test session with 100 element latencies for each subject (20 trials \times 5 serial positions), data points that fell more than two standard deviations from the mean were eliminated from analyses. By this criterion, six latencies were eliminated for Windsor, and 8 for Winston. For assessing within-subject changes during training, paired- t statistics or repeated measure analyses of variance were used. Preferences between members of the chain were assessed using the sign test.

Results

Figure 1 presents latencies for each tamarin during the first three and last three sessions of training, and during the random test session. During training, Windsor's performance was characterized by long latencies to A and shorter latencies throughout the rest of the chain, particularly to E. This pattern was evident within the first three sessions. Total chain time, measured from the presentation of A until a response to E, decreased from 35.9 sec to 28.4 sec between the first three and final three training sessions, but this difference was not significant ($p > .05$). It is clear from Figure 1 that total chain time was composed principally of the latency to A. As that latency may include inattention to the start of a trial, a second latency measure, chain running time, was used to assess changes during training. Windsor's running time, measured from a response to A until a response to E, also did not show changes during training, averaging 15.9 sec in Sessions 1–3, and 17.2 sec during the last three sessions. As can be seen in the middle data set for Windsor, his latencies during the 20 chain trials that preceded the 20 random trials were lower than those observed at the end of training, indicating that the sessions of pairwise testing that preceded the random test session had not disrupted chain performance. Total chain time averaged 10.4 sec during these 20 chain trials. This value was significantly lower than mean chain time at the end of training ($p < .01$). Similarly, chain running time decreased significantly, to 5.67 sec ($p < .05$).

During the 20 random trials, Windsor's latencies, summed across the 20 trials of the random test, averaged 18.8 sec, a value significantly higher than the latencies of the 20 chain trials during this session ($p < .01$). Two analyses of latencies during the random test, one for elements and the other for serial positions, are given in Figure 1. These analyses are a consequence of the fact that the random test dissociates serial positions and elements. In training, elements and serial positions were combined, that is, each element always occurred in the same serial position. In the elements analysis, average latency of each element, A through E, is

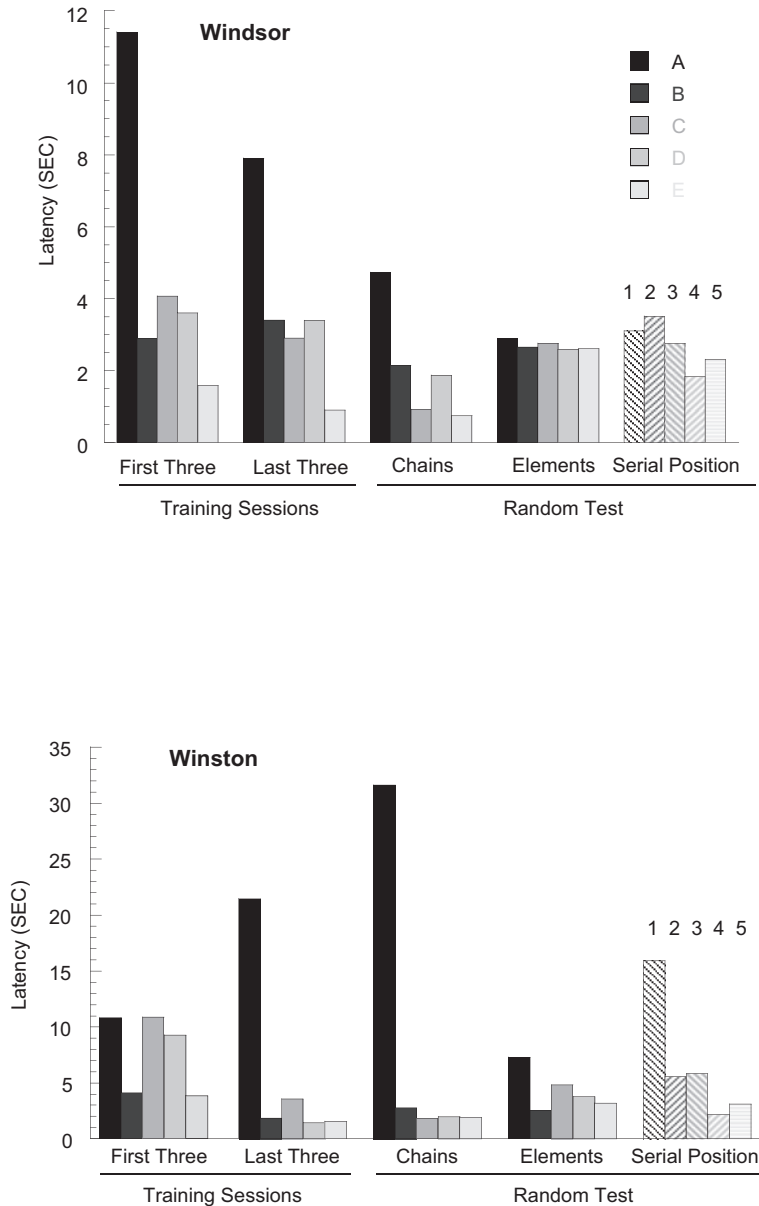


Figure 1. Latencies during the first three and last three training sessions for each element in the five-element chain, and during the random test session. The random test session consisted of 20 chain trials followed by 20 trials in which elements of the chain were randomly presented. Two analyses of performance during the random test are presented. The data set labeled “Elements” refers to the average latency of each element (e.g., A, B, etc.) during random trials. Each element occurred four times at each serial position during random trials. Each column in this data set represents the average of all these presentations. The right-hand data set labeled “Serial Position” gives average latencies at each serial position. Each column presents all element presentation at that serial position during the random test.

given. Each element was presented at each serial position four times during the random test. For Windsor, there was a decrease in latencies for element A, the element with the longest latencies in training, and an increase in the latencies to each remaining element. The result was that all element latencies were equal. The second analysis of random test latencies consists of average latencies at each serial position (1 through 5). The data point for each

serial position in this analysis is composed of the latencies of all elements at that serial position. Chain running time was calculated from this serial position data set, as the time beginning with a response to the element in the first serial position, and ending with a response to the element in the fifth serial position. There was a significant increase in chain running time compared to training, to 13.7 sec ($p < .01$). There was also a tendency for early serial

positions to be associated with higher latencies than were later positions, suggesting that serial position itself may have influenced latencies. The regression of latency on serial position was not significant ($p > .10$), but four of the five individual elements, A through D, evidenced higher average latencies at positions 1 and 2, than at positions 4 and 5.

For Winston, there was no strong control exerted by the different elements in the chain during the first three sessions, but a clear pattern of long latencies to A and shorter latencies to E emerged by the last three training sessions. Total chain latencies averaged 38.0 sec during the first three sessions and 29.8 sec during the last three training sessions. This comparison was not significant ($p > .05$), but these total latencies masked a shift in control exerted by the elements of the chain during this period. Latencies to A increased during training, whereas running time latencies decreased, from 27.4 sec early in training to 8.4 sec by the end of training ($p < .05$).

Winston's average latency across the 20 chain trials in the random test session was not different than his performance at the end of training ($p > .05$), although there was a nearly 10-sec increase in latency to element A. Latencies during the random test averaged 32.6 sec, a value that was not different from the average of the 20 chain latencies that preceded the random test. The lack of difference between these two latencies masked a redistribution of latencies during random trials. As shown in the analysis of elements, latencies to A decreased, whereas latencies to the remaining elements increased. The result was a significant increase in chain running time, to 16.7 sec, compared with running time latencies during the preceding 20 chains ($p < .05$). As shown in the analysis of serial position, Winston's latencies reflected control by serial position during the random test. The regression of latency on serial position was significant ($p < .01$), and for each element, latencies to serial positions 1 and 2 were higher than latencies recorded at positions 4 and 5.

The latency data indicated that both subjects developed appreciation for the elements of the chain. The preference data obtained during pairwise testing supported this conclusion. Three aspects of the preference data are shown in Figure 2. The top panel shows the likelihood of choosing an element as a function of that element's position in the chain. Both tamarins evidenced a pattern of choosing the later elements in the chain over the early elements. The result was also an orderly increase in the likelihood of choosing an element as a function of that element's position in the chain. The regression of choice on element position was significant for each tamarin ($p < .05$). We also examined whether extended pairwise testing had altered preference by comparing the full preference test of 20 presentations of each pair, with the first 10 pairwise presentations. The slopes, intercepts, and multiple R s of the regressions were all highly similar for each tamarin, suggesting that extended testing, and the practice of reinforcing any preference response, had not altered preference patterns. (For Windsor, whole test: slope = .15, intercept = .03, $R = .98$; first half: slope = .17, intercept = -.03, $R = .97$; for Winston, whole test: slope = .15, intercept = .13, $R = .85$; first half: slope = .15, intercept = .07, $R = .81$).

In the middle panel, it can be seen that the likelihood of choosing a later element was related to the distance between the elements of the pair. For each tamarin, choice of the later element of a pair was significantly above chance even for adjacent items such as A and B ($p < .05$), and that likelihood increased as a

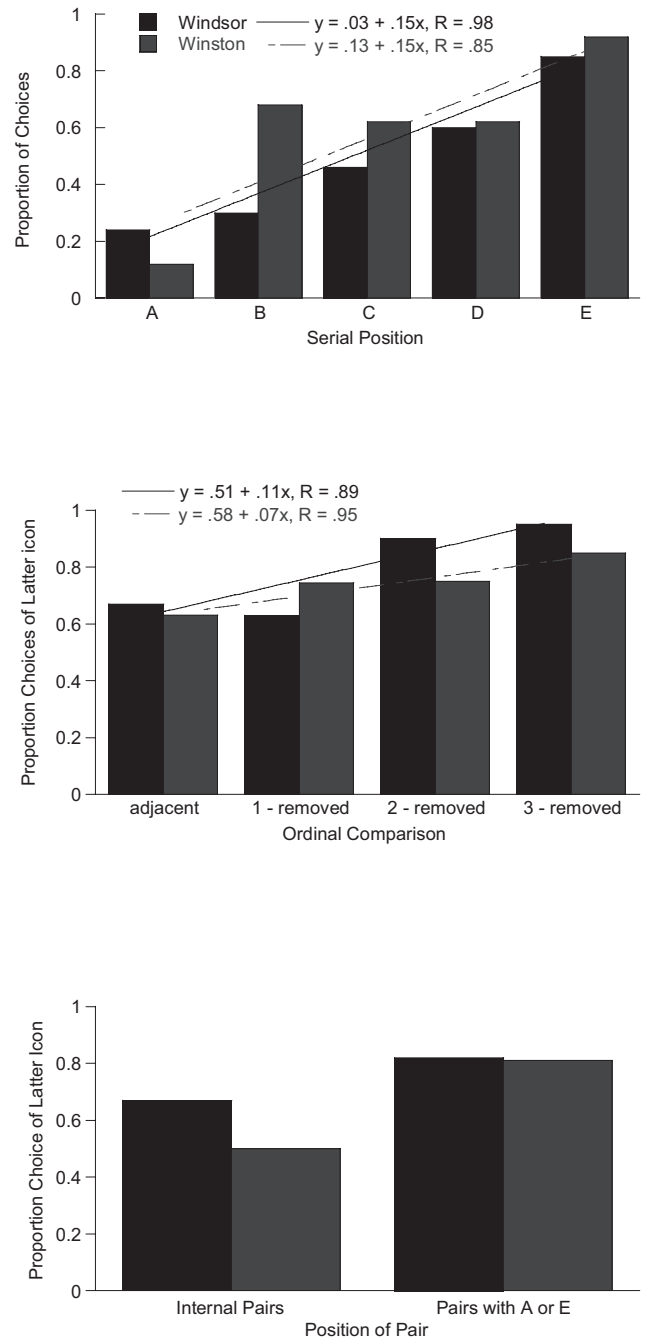


Figure 2. Three aspects of the results from the pairwise testing that followed training. The top panel shows the proportion of choices for each element, averaged across the first 20 pairwise tests that involved each element. The middle panel gives the likelihood of choosing the later element of a pair as a function of the distance between pairs. The bottom panel shows the proportion of choices of a later element in a pair as a function of whether the pair contained an end element (A or E), or consisted solely of internal elements (B/C, B/D, C/D).

function of the increasing distance between pairs. The regression of the likelihood of choosing a later element on pair-distance was significant for each tamarin ($p < .05$).

The bottom panel of Figure 2 indicates that each tamarin was more likely to choose a later element if a pair included an end element (A or E), compared to pairs that were composed of internal elements (B/C, B/D, or C/D). For Windsor, this difference was not reliable ($p > .05$). For Winston, who was indifferent when the comparison involved only interior elements (i.e., choice of a later element was not different than .50), this difference was reliable ($p < .05$).

In summary, during training, latencies to earlier elements in the chain were longer than were latencies to later elements for each tamarin. The random test disrupted this pattern in each tamarin, such that there was a decrease in latency for the first element in the chain, accompanied by increases in latency for the remaining elements. There was evidence in each tamarin that latency tracked serial position during the random test, with the result that earlier serial positions tended to be associated with longer latencies than were later serial positions. The results of the pairwise tests revealed three patterns: First, each tamarin chose later elements in the chain over earlier elements; second, each tamarin was more likely to choose the later element of a pair the further apart the two elements were in the chain; and, third, each tamarin was more likely to choose a later element if the test pair included an end element.

Discussion

These data indicate that in the absence of explicit reinforcement to learn the elements in a serial chain, the tamarins came to appreciate the position of the elements in the chain. The results resemble in some respects those obtained from serial chaining and transitive inference studies in which acquisition of the chain is produced via extensive reinforcement of element pairs (e.g., A+/B-, B+/C-, etc., in which + designates which element in the pair is reinforced). Given that our results were obtained without differential reinforcement of one element over another, they suggest that exposure to sequential information in itself results in the development of appreciation for that information. To be sure, knowledge of this implicit chain was not identical to the knowledge evident in standard serial chaining and transitive inference studies. In many but not all cases in which these procedures have been studied, there appears to be more precise control over internal pair choices (e.g., B/D) than were evident in this study (Figure 2, bottom panel; Gillan, 1981; Lazareva, Smirnova, Zorina, & Rayevsky, 2001; Terrace & McGonigle, 1994). Other aspects of performance were similar, including the presence of what has been called the symbolic distance effect, the finding that pairwise choices are more accurate the further apart the elements (Figure 2, middle panel; D'Amato & Colombo, 1990).

A thorough specification of what was learned in this procedure must await further study. The data indicate that the tamarins did not learn something as simple as "Touch the icon and reinforcement comes periodically." If so, there would have been no differential control exerted by the elements of the chain, and no disruption during the random test. It appears that the tamarins also did not learn a variant of this rule that might be something like: "Reinforcement comes after every fifth response." This type of rule does not require appreciation of the elements in the chain, but instead invokes a form of ordinal counting. If adopted, this rule also would not have produced the pattern of results in the pairwise

tests, nor the disruptions evident during the random test, since the structure of five serially presented icons followed by reinforcement was maintained during the random test.

Since reinforcement came at the end of each chain, and stimulus preferences and latencies favored the later portions of the chain, the most straightforward interpretation of this pattern of results is that they reflect the associative strength of the individual elements. It may be that a complete account will also include the idea that the tamarins had available something like an ordinal template in which each serial position was appreciated differently, irrespective of which element appeared in that position. Evidence for this idea comes from the serial position results during the random test, in which early positions tended to be associated with higher latencies than were later positions. This idea is consistent with the conclusions drawn from a number of chaining and transitive inference studies. There are, though, interpretations that rely solely on associative strength (compare Chen, Swartz, & Terrace, 1997, and Lazareva et al., 2001, with Wynne, 1997).

What the tamarins may have expected cannot be determined from this study alone, but the implicit chains procedure provides techniques for exploring that question. One could dissociate associative strength from the idea of an ordinal template by presenting reinforcement randomly throughout the chain, but maintaining the stimulus pattern. This manipulation would convert the procedure into a type of discrete-trial random-ratio schedule of reinforcement. If performance reflects principally associative strength, the rule adopted by subjects might be in the form of, "Reinforcement may come following any icon, so treat them equally." By this rule, subjects should be indifferent to the pattern. On the other hand, if they learned something about the serial nature of the chain, training latencies, element preferences, and the results of the random test should reflect that learning, irrespective of the fact that the pattern per se does not predict reinforcement.

Another interpretative problem derives from the fact that in this procedure a behavioral pattern is correlated with the stimulus pattern. Perhaps the learning in this procedure is principally behavioral, not perceptual. SRT procedures are often, though not universally understood as motor in nature (e.g., Deroost & Soetens, 2006). This possibility can be studied by altering the procedure so that the elements are different visual icons that appear in the same order on each trial, but can be displayed at any location. This manipulation maintains the perceptual pattern, but dissociates it from any behavioral pattern.

These examples illustrate some of the features of implicit chaining that make it a useful addition to the technology available in the study of serial behavior. Perhaps most importantly, the ability to evaluate individual elements allows a more precise specification of what is learned in this procedure compared to traditional SRT tasks. That advantage may reveal aspects of that learning that are not observed in the typical SRT procedure. Winston's random test, for example, evidenced no overall increase in latencies, a result that would usually be taken to indicate an absence of sequence learning. Yet that result masked a significant redistribution of latencies, one that would have gone undetected if element analyses had not been possible.

It should be added that implicit chaining and other nonhuman analogs of implicit learning may be important additions to the study of comparative cognition. There are at present a growing body of such procedures to which the present results belong (e.g.,

Domenger & Schwarting, 2004; Fitch & Hauser, 2004; Froehlich et al., 2004; Gentner et al., 2006). Implicit learning has been characterized as a type of nondeclarative or procedural learning that can be contrasted with declarative or explicit learning. Non-human analogs of declarative procedures comprise many of the tasks studied in comparative cognition. There are a number of indications that implicit learning has different cognitive characteristics compared to declarative learning, and is subserved by different neurological mechanisms (Bischoff-Grethe, Goedert, Willingham, & Grafton, 2004; Jiménez, Vaqueo, & Lupiáñez, 2006). Interesting to note, in humans some forms of implicit learning, including SRT tasks, are conserved in cases of amnesia, while declarative learning is diminished. Conversely, SRT learning is degraded in Parkinson's patients, whereas declarative learning is largely conserved (Nissley & Schmitter-Edgecombe, 2002).

References

- Bischoff-Grethe, A., Goedert, K. M., Willingham, D. T., & Grafton, S. T. (2004). Neural substrates of response-based sequence learning using fMRI. *Journal of Cognitive Neuroscience*, *16*, 127–138.
- Chen, S., Swartz, K. B., & Terrace, H. S. (1997). Knowledge of the ordinal position of list items in rhesus monkeys. *Psychological Science*, *8*, 80–86.
- Clegg, B. A., DiGirolamo, G. J., & Keele, S. W. (1998). Sequence learning. *Trends in Cognitive Sciences*, *2*, 275–281.
- Crofts, H. S., Muggleton, N. G., Bowditch, A. P., Pearce, P. C., Nutt, D. J., & Scott, E. A. M. (1999). Home cage presentation of complex discrimination tasks to marmosets and rhesus monkeys. *Laboratory Animal*, *33*, 207–214.
- D'Amato, M. R. (1991). Comparative cognition: Processing of serial order and serial pattern. In L. Dachowski & C. F. Flarherty (Eds.), *Current topics in animal learning: Brain, emotion and cognition* (pp. 165–185). Hillsdale, NJ: Erlbaum.
- D'Amato, M. R. & Colombo, M. (1990). The symbolic distance effect in monkeys (*Cebus apella*). *Animal Learning & Behavior*, *18*, 133–140.
- Deroost, N. & Soetens, 2006. Perceptual or motor learning in SRT tasks with complex sequence structures. *Psychological Research*, *70*, 88–102.
- Domenger, D., & Schwarting, R. K. W. (2005). Sequential behavior in the rat: A new model using food-reinforced instrumental behavior. *Behavioural Brain Research*, *160*, 197–207.
- Dusek, J. A., & Eichenbaum, H. (1997). The hippocampus and memory for orderly stimulus relations. *Proceedings of the National Academy of Sciences, USA*, *94*, 7109–7114.
- Fitch, W. T., & Hauser, M. D. (2004). Computational constraints on syntactic processing in a nonhuman primate. *Science*, *303*, 377–380.
- Froehlich, A. L., Herbranson, W. T., Lopez, J. D. (2004). Anticipating by pigeons depends on local statistical information in a serial response time task. *Journal of Experimental Psychology: General*, *133*, 31–45.
- Gentner, T. Q., Fenn, K. M., Margoliash, D., & Nusbaum, H. C. (2006). Recursive syntactic pattern learning by songbirds. *Nature*, *440*, 1204–1207.
- Gillan, D. J. (1981). Reasoning in the chimpanzee: II. Transitive inference. *Journal of Experimental Psychology: Animal Behavior Processes*, *7*, 150–164.
- Hunt, R. H., & Aslin, R. N. (2001). Statistical learning in a serial reaction time task: Access to separable statistical cues by individual learners. *Journal of Experimental Psychology: General*, *30*, 658–680.
- Jiménez, L., Vaqueo, J. M. M., & Lupiáñez, J. (2006). Qualitative differences between implicit and explicit sequence learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *32*, 475–490.
- Lazareva, O. F., Smirnova, A. A., Zorina, Z. A., & Rayevsky, V. V. (2001). Hooded crows solve a transitive inference problem cognitively. *Animal Welfare*, *10*, 219–231.
- Nissley, H. M., & Schmitter-Edgecombe, M. (2002). Perceptually based implicit learning in severe closed-head injury patients. *Neuropsychology*, *16*, 111–122.
- Reber, A. S. (1967). Implicit learning of artificial grammars. *Journal of Verbal Learning and Verbal Behavior*, *6*, 855–863.
- Robbins, T. W. (2002). The 5-choice serial reaction time task: Behavioural pharmacology and functional neurochemistry. *Psychopharmacology*, *163*, 262–380.
- Rowland, L. A., & Shanks, D. R. (2006). Sequence learning and selection difficulty. *Journal of Experimental Psychology: Human Perception and Performance*, *32*, 287–299.
- Seger, C. A. (1994). Implicit learning. *Psychological Bulletin*, *115*, 163–196.
- Swartz, K. B., Chen, S., & Terrace, H. S. (1991). Serial learning by Rhesus monkeys. I. Acquisition and retention of multiple four-item lists. *Journal of Experimental Psychology: Animal Behavior Processes*, *17*, 396–410.
- Terrace, H. (2001). Chunking and serially organized behavior in pigeons, monkeys and humans. In R. G. Cook (Ed.), *Avian visual cognition*. Retrieved January 14, 2008, from www.pigeon.psy.tufts.edu/avc/terrace/
- Terrace, H. S., & McGonigle, B. (1994). Memory and representation of serial order by children, monkeys, and pigeons. *Current Directions in Psychological Science*, *3*, 180–189.
- Treichler, F. R., & Van Tilburg, D. (1996). Concurrent conditional discrimination tests of transitive inference by Macaque monkeys: List linking. *Journal of Experimental Psychology: Animal Behavior Processes*, *22*, 105–117.
- Wright, A. A., Santiago, H. C., Sands, S. F., Kendrick, D. F., & Cook, R. G. (1985). Memory processing of serial lists by pigeons, monkeys, and people. *Science*, *229*, 287–289.
- Wynne, C. (1997). Pigeon transitive inference: Tests of simple accounts of a complex performance. *Behavioural Processes*, *39*, 95–112.

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