

Reversal Learning in Rats (*Rattus norvegicus*) and Pigeons (*Columba livia*): Qualitative Differences in Behavioral Flexibility

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Research has shown that pigeons given a simultaneous visually based discrimination reversal, in which a single reversal occurs at the midpoint of each session, consistently show anticipation prior to the reversal as well as perseveration after the reversal, suggesting that they use a less effective cue (time or trial number into the session) than what would be optimal to maximize reinforcement (local feedback from the most recent trials). In the present research, pigeons (*Columba livia*) and rats (*Rattus norvegicus*) were tested with a simultaneous spatial discrimination midsession reversal. Pigeons showed remarkably similar errors in anticipation and perseveration as with visual stimuli, thereby continuing to show the suboptimal use of time as a cue, whereas rats showed no anticipatory errors and very few perseverative errors, suggesting that they used local feedback as a cue, thus more nearly optimizing reinforcement. To further test the rats' flexibility, they were then tested with a variable point of reversal and then with multiple points of reversal within a session. Results showed that the rats effectively maximized reinforcement by developing an approximation to a win–stay/lose–shift rule. The greater efficiency shown by rats with this task suggests that they are better able to use the feedback from their preceding choice as the basis of their future choice. The difference in cue preference further suggests a qualitative difference in acquisition of the midsession reversal task between pigeons and rats.

Keywords: reversal learning, simultaneous discrimination, win–stay/lose–shift, rats, pigeons

Animals frequently are confronted with changes in their natural environment. Often these changes occur in the availability of resources, as some patches are depleted and others are replenished at varying rates. The variability in environmental demands has been thought to affect the behavioral flexibility of an organism, which in turn is believed to be associated with higher levels of cognition (Bitterman, 1965; Bond, Kamil, & Balda, 2007).

An ecological approach to behavioral flexibility would focus on its adaptive value. If an animal can rely on genetically predisposed behavior, flexibility would not be necessary; however, in a rapidly changing environment, predisposed behavior may not be the most adaptive. Specifically, environments that may change rapidly in unpredictable ways should select for flexible behavior by animals that occupy that niche (see Bond et al., 2007, for a review). Flexibility may evolve for specific environmental demands, such as food preferences. For example, many species of birds have evolved to eat a variety of seeds and berries, whereas rats apparently have had more competition and have for this reason evolved an extremely diverse and flexible food repertoire, such that they base their food preferences (and avoidances) on the consequences of digestion (i.e., foods that do not induce illness will be eaten

again; Zentall, 2000). Similar to rats, humans have evolved an extremely diverse food repertoire and also base the consumption of food on the consequences of digestion. Additionally, the development of language by humans has allowed them to communicate to each other about appropriate and inappropriate foods.

A simple measure of behavioral flexibility is the rate at which an animal can reverse a previously acquired discrimination. If one trains an animal on a simultaneous discrimination and then reverses the discrimination (the positive stimulus, S+, becomes the negative stimulus, S-, and the S- becomes the S+), the animal must learn to reassign its responses to adjust to the change in contingencies. One can then compare the rate of reversal learning to the rate of original learning (Bitterman, 1965, 1975) to obtain a measure of behavioral flexibility (e.g., the transfer index Rumbaugh & Pate, 1984; DeLillo & Visalberghi, 1994; Washburn & Rumbaugh, 1991). A related measure of cognitive capacity (or intelligence), called serial reversal learning (Mackintosh, 1974), is the improvement in learning when the discrimination is repeatedly reversed (Bitterman, 1965, 1975).

A variety of nonhuman animals have been tested for their improvement in rate of reversal learning with successive reversals (Warren, 1965, 1973), and researchers have argued that differences in the rate of learning serial reversals (measured by the decline in number of trials to reach a criterion level of discrimination performance) reflect quantitative differences consistent with the ordering of different species along an evolutionary scale, such that the improvement is greatest for primates, less so for other mammalian species, such as rats, even less so for birds and reptiles, and almost absent for fish and invertebrates (Bitterman & Mackintosh, 1969; Gossette, Gossette, & Riddell, 1966; Mackintosh, 1965,

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1969; Mackintosh, McGonigle, Holgate, & Vanderver, 1968). Mackintosh et al. (1968) proposed that the differences among species reflected varying abilities, in general, to maintain attention to relevant stimulus dimensions. If animals learn to attend only to their recent history of reinforcement, they could learn to adjust rapidly to changes in contingencies, thereby producing behavior that is suggestive of a win-stay/lose-shift rule, thus maximizing reinforcement. When optimally applied, this rule-based strategy consists of choosing the stimulus to which responding was reinforced on the previous trial (win-stay) and switching to the alternative stimulus following a single unreinforced response (lose-shift; Levine, 1959).

Although the most common procedure for studying serial reversal learning has used between-session reversals, in which subjects must achieve a criterion accuracy level prior to a given reversal, Mackintosh et al. (1968) trained one group of rats on a within-session reversal, in which the reversal always occurred in the middle of the session. It was found that the rats began sessions responding nondifferentially, meaning the subjects were not remembering which stimulus was correct from the previous day (see also Cook & Rosen, 2010) and, although there was some improvement with training, subjects never achieved the level of criterion performance that they had during the original discrimination.

Rayburn-Reeves, Molet, and Zentall (2011), modified Mackintosh et al.'s (1968) midsession reversal task by using a simultaneous visual discrimination with red and green hues, with the exception that, instead of sessions beginning with the stimulus which was most recently correct on the previous session, each session began with the same stimulus correct. In Rayburn-Reeves et al.'s (2011) procedure, for each pigeon, one stimulus was randomly assigned as the first correct stimulus (S1) and responses to that stimulus and not the other (S2) were reinforced for the first half of an 80-trial session (S1+, S2-), with contingencies reversed for the last half of the session (S1-, S2+). Results showed that the pigeons made two distinct types of errors: anticipatory errors (choosing S2 prior to the reversal) and perseverative errors (choosing S1 after the reversal). This pattern of results suggests that the pigeons were not very sensitive to the feedback from the outcome of the most recent trials and were using the time or number of trials into the session as a cue to estimate the point of reversal. In an attempt to reduce the relevance of the timing cue, Rayburn-Reeves et al. (2011) conducted a new experiment with a variable reversal procedure in which the reversal location varied in an unpredictable manner over sessions. Specifically, in each session the reversal occurred at one of five different locations (after Trial 10, 25, 40, 55, or 70). After 100 sessions of training, results indicated that when the reversal occurred early in the session, the pigeons showed a large number of perseverative errors but few anticipatory errors and when the reversal occurred late in the session, the pigeons showed a large number of anticipatory errors but few perseverative errors. In addition, surprisingly, the total number of errors increased the further from the middle of the session the reversal occurred. Thus, even when the reversal location was unpredictable, time into the session continued to influence both anticipatory and perseverative errors. Furthermore, when the reversal occurred at an unpredictable point in the session, the total number of errors actually increased relative to when the reversal occurred at a predictable point in the session.

The previous experiments by Rayburn-Reeves et al. (2011) with pigeons used a visual discriminations, however, there is evidence that pigeons show greater improvement with serial reversals involving spatial discriminations than with visual discriminations (Bullock & Bitterman, 1962; Weyant, 1966). It is possible that a spatial midsession reversal procedure might be more analogous to natural foraging behavior as it pertains to the distribution and depletion of food that is spatially distributed. Therefore, it is possible that the midsession reversal involving a spatial discrimination would create greater sensitivity to the reversed contingencies.

Experiment 1

The purpose of Experiment 1 was to compare performance on a spatial midsession reversal for pigeons, as compared with the visual midsession reversal used by Rayburn-Reeves et al. (2011). In the first experiment we asked whether a spatial midsession reversal task would produce greater sensitivity to the changing reinforcement conditions.

Method

Subjects

Eight white Carneaux pigeons (*Columba livia*) ranging in age from 2 to 12 years served as subjects. All subjects had been given experience in previous unrelated studies involving simultaneous color and spatial discriminations, but they had never been exposed to a discrimination reversal procedure. Subjects were maintained at 85% of their free-feeding weight throughout the experiment, and individually housed in wire cages with free access to water and grit in a colony room that was maintained on a 12-hr/12-hr light/dark cycle. The pigeons were maintained in accordance with a protocol approved by the Institutional Animal Care and Use Committee at the University of Kentucky.

Apparatus

The experiment was conducted in a BRS/LVE (Laurel, MD) sound-attenuating operant test chamber measuring 34 cm high, 30 cm from the response panel to the back wall, and 35 cm across the response panel. Three circular response keys (2.5 cm diameter) were aligned horizontally on the response panel and were separated from each other by 6.0 cm, but only the left and right side keys were used in this experiment. The bottom edge of the response keys was 24 cm from the wire-mesh floor. A 12-stimulus in-line projector (Industrial Electronics Engineering, Van Nuys, CA) with 28-V, 0.1-A lamps (GE 1820) that projected a white light (no filter) was mounted behind each response key. Mixed-grain reinforcement (Purina Pro Grains—a mixture of corn, wheat, peas, kafir, and vetch) was provided from a raised and illuminated grain feeder located behind a 5.1 × 5.7 cm aperture horizontally centered and vertically located midway between the response keys and the floor of the chamber. Reinforcement consisted of 1.5-s access to mixed grain. The experiment was controlled by a microcomputer and interface located in an adjacent room.

Procedure

At the start of each experimental session, both the left and right response keys were illuminated white, indicating the start of the first trial. For half of the subjects, a single response to the left key (S1) turned off both keys and resulted in 1.5-s access to food, followed by a 3.5-s dark intertrial interval (ITI), whereas a response to the right key (S2) immediately turned both stimuli off and resulted in a 5-s dark ITI. For the other half of the subjects, choice of the right key (S1) was reinforced and not the left key (S2). For the first 40 trials of each 80-trial session, subjects were trained with S1+/S2-. From Trial 41 to Trial 80, the contingencies were reversed (S2+/S1-). Subjects were trained for 50 sessions.

Results and Discussion

Pigeons reached a stable level of choice accuracy in about 20 sessions of training. The percentage choice of the first correct stimulus (S1) as a function of trial number (in blocks of five trials)

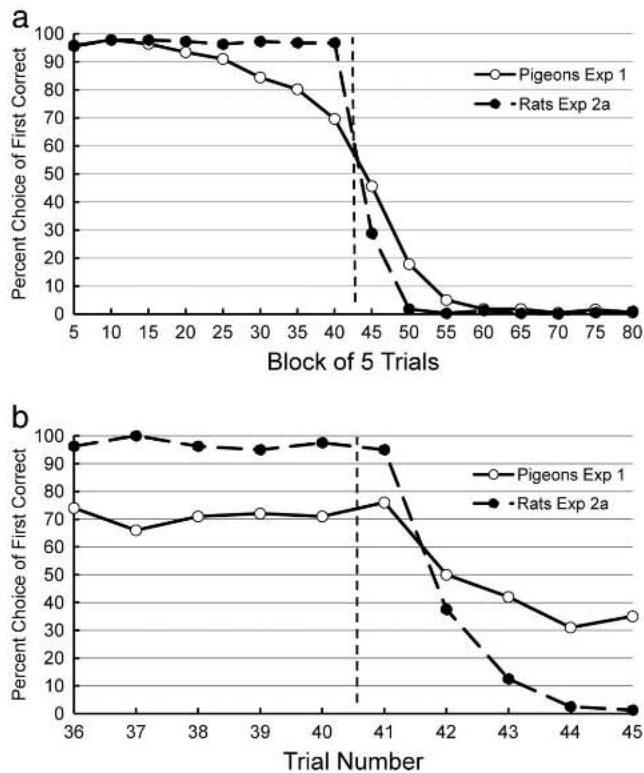


Figure 1. (a.) Experiment 1 and 2a. Percentage choice of the first correct stimulus (S1) averaged across subjects as a function of trial number for the last 10 sessions of training (Sessions 41–50) for the pigeons (Experiment 1; open circles) and for the rats (Experiment 2a; closed circles) for the midsession spatial reversal. The dotted line indicates the point at which the reversal occurred in the session. (b.) Experiment 1 and 2a. Percentage choice of the first correct stimulus (S1) as a function of trial number for Trials 36–45, averaged across subjects, for the last 10 sessions of training (Sessions 41–50) for the pigeons (Experiment 1; open circles) and for the rats (Experiment 2a; closed circles) for the midsession spatial reversal. The dotted line indicates the point at which the reversal occurred in the session.

averaged over subjects for the last 10 training sessions appears in Figure 1a. As can be seen in the figure, the pigeons chose S1 almost exclusively during early trials in each session, choice of S1 then declined prior to the reversal and continued to decline to almost exclusive choice of S2 following the reversal. As can be seen in Figure 1a, accuracy was only about 70% correct (choice of S1) during the five trials immediately before the reversal and it was only about 54% correct (46% choice of S1) during the five trials immediately following the reversal.

A more-detailed view of the pigeons' sensitivity to the reversal can be seen in the trial-by-trial plot of choice of the first correct stimulus over the block of trials immediately prior to the reversal (Trials 36–40) and immediately after the reversal (Trials 41–45) presented in Figure 1b. The average drop in choice of S1 from Trial 41 to 42 was 26% and it averaged 0.4% over the five trials prior to the reversal as well as the first reversal trial (Trials 36–41). The mean decline in choice of S1 on those trials immediately prior to the reversal, as compared with the decline in choice of S1 between Trial 41 and 42, was statistically reliable, $t(9) = 4.09, p = .003$. Thus, there was some effect of the feedback from Trial 41, beyond the general trend that the pigeons had, to choose S2 as the session progressed. However, the average drops from Trial 42 to 43, Trial 43 to 44, and Trial 44 to 45 were not statistically significant $t(9) = 1.18, p > .1, t(9) = 2.18, p > .05$, and $t(9) = .58, p > .1$, respectively. To get a measure of the degree to which the pigeons came close to the ideal win-stay/lose-shift pattern of choice we examined the mean accuracy on Trials 36 to 45 with accuracy on Trial 41 (the outcome of which was the first cue to shift) omitted. Mean accuracy on those nine trials pooled over Sessions 41–50 was 66.2% correct, a little better than the pigeons in Rayburn-Reeves et al. (2011) which were at 58.0% correct; however, the overall pattern of responding for pigeons in Experiment 1 and that from Rayburn-Reeves et al. (2011) was quite similar.

The results of Experiment 1 indicate that when given a simple spatial discrimination in which a single reversal occurs at the midpoint of each session, pigeons continue to show anticipation errors prior to the reversal and perseveration errors after the reversal. Although pigeons showed some sensitivity to the feedback from the first nonreinforced trial, it was substantially less than optimal.

If one were to plot the pigeons' choice of S2 as a function of trials into the session, the resulting plot would look not unlike the scallop-shaped plot of response rate by pigeons (or rats) responding on a fixed interval schedule. Although time into the session is a relatively reliable cue to the reversal, given the much less efficient ability of organisms to time (or count that many trials), a much more effective cue as a signal for the reversal would be the presence (or absence) of reinforcement on the immediately preceding trial(s).

The results of Experiment 1 indicate that pigeons do not use the information afforded by local feedback as efficiently as they might to maximize reinforcement. These results parallel those found by Rayburn-Reeves et al. (2011) in which pigeons given a simple simultaneous discrimination, midsession reversal with red and green hues showed both anticipatory and perseverative errors. The fact that pigeons in Experiment 1 showed results similar to that of Rayburn-Reeves et al. (2011) suggests that, regardless of the nature of the discrimination, pigeons appear not to be using the

most relevant cues in reversing their choice of stimulus based on the feedback from the immediately preceding trials. The consistency with which all birds displayed both anticipatory and perseverative errors in the present spatial midsession reversal task, suggests that pigeons are predisposed to adopt a time-based strategy with this task. This conclusion is supported by the similarity of the present results to those of Rayburn-Reeves et al.'s (2011) midsession reversal with visual cues, whether or not the reversal location varies unpredictably. Furthermore, it suggests that pigeons have a relative insensitivity to the immediate feedback of the outcome of the previous trial.

Rats and pigeons have been the most commonly tested nonhuman species used by experimental psychologists in laboratory research, and they have been used often interchangeably in studies investigating cognitive abilities. For example, when tested under comparable conditions, rats and pigeons show very similar cognitive abilities in timing and memory (Green, Myerson, Holt, Slevin, & Estle, 2004), and numerical competence (Capaldi & Miller, 1988; Rayburn-Reeves, Miller, & Zentall, 2010), as well as a variety of other learning tasks. Both pigeons and rats have also been shown to display progressive improvement in serial reversal learning tasks when tested under optimal conditions (Nigrosh, Slotnick, & Nevin, 1975; Slotnick, Kufera, & Silberberg, 1991; Duncan & Slotnick, 1990). Thus, there is reason to believe that the cognitive abilities of rats and pigeons are, at least qualitatively, quite similar. Additionally, because rats and pigeons have been shown to produce similar levels of accuracy in both timing and counting procedures, it would be interesting to see whether rats employ the same predisposition toward timing the predictable reversal location. The purpose of the present research was to test this conclusion in a somewhat different context.

Experiment 2a

The purpose of Experiment 2a was to investigate whether rats would also show a preference for a time-based cue to solve the spatial midsession reversal as pigeons appeared to be doing, or whether they would use a more appropriate local feedback cue to maximize overall reinforcement.

Subjects

Eight albino rats (Sprague-Dawley, *Rattus norvegicus*), 6–12 months old, obtained from Harlan Laboratories (Indianapolis, IN), were used as subjects. All subjects had been previously trained to lever press. The rats were maintained at 85% of their free-feeding weight throughout the experiment. They were housed in pairs in polystyrene cages with free access to water in a colony room that was maintained on a 12-hr/12-hr light/dark cycle. The rats were maintained in accordance with a protocol approved by the Institutional Animal Care and Use Committee at the University of Kentucky.

Apparatus

The experiment was conducted in a standard rodent operant chamber (Coulbourn Instruments, Lehigh Valley, PA) measuring 25.7 cm across the response panel, 33 cm from ceiling to floor, and 31 cm from response panel to the back wall. The chamber had a

white house light, centered on the response panel and located 1.3 cm from the ceiling. A pellet dispenser delivered pellets to a food well that was centered on the response panel, 5.6 cm from the floor. Two response levers, 3.6 cm wide, were located on either side of the food well; each located 2.3 cm from the wall and 5.6 cm from the floor. Reinforcement consisted of one pellet (MLab Rodent Tablet 45 mg 1811156, TestDiet, Richmond, IN) for each correct response. The experimental chamber was located in a small isolated room to reduce extraneous visual and auditory stimulation. The experiment was controlled by a microcomputer and interface located in an adjacent room.

Procedure

At the start of each experimental session, the house light was illuminated, indicating that both levers were operable. For half of the subjects, a single response to the left lever (S1) resulted in the feeder light turning on and a single pellet being delivered to the food well. After 2 s, both the feeder light and house light turned off for a 3-s dark ITI. If the rat chose the right lever (S2), the house light turned off for a 5-s dark ITI and no food was delivered. Immediately following the ITI, the house light turned on indicating the start of the next trial. For the other half of the subjects, choice of the right lever (S1) and not the left (S2) was reinforced. For the first 40 trials of each 80-trial session, subjects were trained with S1+/S2-. On Trial 41 and for the remainder of the session, the contingencies were reversed (S2+/S1-). Subjects were trained for 50 sessions.

Results and Discussion

The percentage choice of the first correct lever (S1) as a function of trial number, averaged across subjects for the last 10 sessions of training (Sessions 41–50), appears in Figure 1a, together with the pigeon spatial reversal data. The data are plotted in blocks of five trials. As can be seen in the figure, the rats chose S1 almost exclusively during the first half of the session up to the reversal point. On the five trials immediately preceding the reversal, accuracy was 97% correct. For the next five trials, accuracy was at 71% (29% choice of S1). For the remaining blocks of trials after the reversal (Trials 46–80) choice was almost exclusively to S2.

To get a more sensitive measure of the choices just prior to and immediately following the reversal, percentage choice of the first correct lever on a trial-by-trial basis for the five trials before the reversal and the first five trials of the reversal is plotted in Figure 1b. As can be seen in the figure, the rats responded to S1 almost exclusively up to and including Trial 41 (the first trial of the reversal). Accuracy on Trials 42–45 was 62.5%, 87.5%, 97.5%, and 98.8% respectively. The average drop in choice of the first correct stimulus between Trial 41 and 42 was 57.5% and it was negligible over the five trials prior to the reversal (Trials 36–41). Thus, the rats showed virtually no anticipation of the reversal and they showed great sensitivity to the feedback from the first non-reinforced response to S1. Their rapid shift in responding from S1 to S2 following Trial 41 demonstrates their efficient use of the information afforded by the outcome of the first trial of the reversal. Prior to the reversal, the rats' mean accuracy on the five trials immediately preceding the reversal was at 97%, whereas

pigeons' mean accuracy was at 70%. An independent-samples *t* test conducted on the pooled accuracy for the five trials immediately preceding the reversal for the pigeons and rats indicated that the difference was significant $t(16) = 5.36, p < .0001$. A similar analysis on the pooled accuracy for the five trials immediately following the reversal indicated that the difference was also significant, $t(16) = 3.91, p < .001$. Thus, the rats made significantly fewer anticipatory errors prior to the reversal and significantly fewer perseverative errors after the reversal. A final analysis between the rats and the pigeons was conducted on the difference between the five trials immediately preceding and following the reversal for choice of S1. On average, the difference for the rats was 68%, whereas for the pigeons it was 24%, and this difference was statistically reliable $t(16) = 8.43, p < .0001$.

A further measure of how close the rats were to an ideal win-stay/lose-shift pattern of choice is mean accuracy on Trials 36 to 45 with accuracy on Trial 41 (the outcome of which was the first cue to shift) omitted. Mean accuracy on those nine trials over Sessions 41–50 was 92.4% correct. In contrast, for the pigeons in Experiment 1, mean accuracy on those nine trials over Sessions 41–50 was 66.2% correct, and, again, this difference was statistically reliable $t(8) = 11.88, p < .0001$.

The results of Experiment 2a indicate that when rats are given a simple simultaneous spatial discrimination in which a single reversal occurs at the midpoint of each session, they respond almost exclusively to S1 until the reversal, then switch responding to S2 almost immediately, and maintain responding to S2 for the remainder of the session. Thus, rats, unlike pigeons, appear to be able to effectively use local feedback (the outcome of the most recent trial) and approach maximizing reinforcement on subsequent trials. Within one or two reversal trials, rats are able to inhibit responses from a previously correct stimulus that has been repeatedly reinforced over a large number of trials and switch responses to a stimulus that has gone unreinforced for those trials.

To further strengthen the argument that from early in training, pigeons and rats showed markedly different acquisition functions, data from Sessions 1–40 are plotted in 10-session blocks for pigeons (Figure 2a) and rats (Figure 2b). For the five trials prior to the reversal for Sessions 1–10, choice of S1 was 84% for the rats, whereas it was 64% for the pigeons, and this difference was statistically reliable $t(16) = 3.67, p < .002$. Additionally, there was a significantly reliable difference between the five trials prior to and following the reversal on Sessions 1–10 for the rats $t(7) = 5.93, p < .0006$, whereas for the pigeons, the difference was not significant $t(9) = 2.07, p = .075$. Therefore, even early in training, rats showed significant differences in performance and they maintained those differences throughout training.

The results of Experiment 2a indicate that rats come close to using a win-stay/lose-shift rule. This behavior provides evidence that, under these conditions, rats are capable of using the most appropriate information to approximate maximizing reinforcement. However, because the point at which the reversal occurred was consistently at the same point in the session and it occurred only once during the session, it is possible that the predictability of the reversal allowed for greater sensitivity to the change in contingency because the rats could have used more than the outcome from the previous trial on which to base their response (i.e., it is possible that they were better timers or counters than the pigeons).

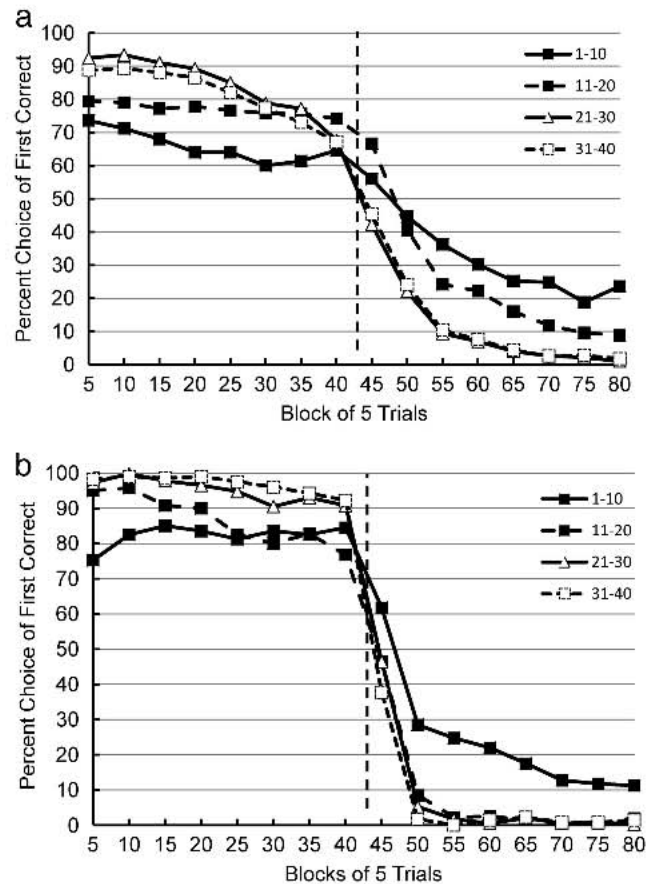


Figure 2. (a.) Experiment 1. Percentage choice of S1 as a function of trial number averaged across pigeons for Sessions 1–40 plotted in 10 session blocks. The dotted line indicates the point at which the reversal occurred in the session. (b.) Experiment 2a. Percentage choice of S1 as a function of trial number averaged across rats for Sessions 1–40 plotted in 10 session blocks. The dotted line indicates the point at which the reversal occurred in the session.

In one such test for greater sensitivity, Rayburn-Reeves et al. (2011) varied the point of reversal for pigeons in an attempt to discourage their use of time as a cue and found that pigeons actually made more errors overall than with the midsession reversal. It appeared that the pigeons tended to average the point of reversal over sessions such that they showed a greater tendency to make perseverative errors when the reversal occurred early in the session and they showed a greater tendency to make anticipatory errors when the reversal occurred late in the session. Thus, one could say that they continued to use time into the session as a cue to reverse. If rats also show an increase in errors with the variable within-session reversal, it would suggest they too use the time into the session as a cue to reverse.

Experiment 2b

The purpose of Experiment 2b was to ask whether making unpredictable the point in the session at which the reversal occurred would disrupt the ability of the rats to maximize reinforcement. If the number of errors increased when the reversal location

varied unpredictably within the session, it would suggest that rats were also using the passage of time as a cue, although perhaps they were using it more efficiently. In Experiment 2b we also asked if the rats' performance would be disrupted if there were more than one reversal per session. If the rats were using something approximating a win-stay/lose-shift rule, an additional reversal during a session should be only temporarily disruptive.

Subjects and Apparatus

The subjects from Experiment 2a served in Experiment 2b. Experiment 2b was conducted 4 weeks following the end of Experiment 2a. The rats were housed and maintained in the same manner as they were in Experiment 2a. The apparatus was the same as that used in Experiment 2a.

Procedure

Refresher sessions. Because the rats had been off task for some time before the start of Experiment 2b, each rat was given four sessions of training, as in Experiment 2a, with the reversal at Trial 41.

Phase 1: Variable location of the reversal in the session. The procedure for Phase 1 of Experiment 2b was the same as in Experiment 2a, however, instead of the reversal always occurring on Trial 41 of each session, the reversal could occur in one of five different locations in the session (after Trial 10, 25, 40, 55, or 70). Because the reversal no longer occurred in a predictable location in the session, other cues such as time or number of trials from the start of the session could not be used as a reliable cue. To the degree that the rats were using cues other than local feedback, varying the location of the reversal in the session should disrupt reversal accuracy. Subjects were given 15 sessions with the variable reversal location procedure (three sessions at each reversal location, randomly selected without replacement).

Phase 2: Variable location of one or two reversals per session. In Phase 2, half of the sessions involved a single reversal at a variable point in the session as in Phase 1. The remaining

sessions involved two reversals that could occur at any two of the reversal points used in Phase 1. For sessions with two reversals, a total of 10 possible combinations of two reversals were generated (see Table 1). Because the addition of a second reversal within a session unbalanced the overall number times S1 and S2 were the S+ stimulus (on a typical session, S1 was correct more often than S2; see Table 1), selected sessions with a single reversal were randomly intermixed throughout the 20 sessions to balance the number of S1 and S2 correct trials, overall. Thus, there were 10 sessions with one reversal per session and 10 sessions with two reversals per session.

Phase 3: Variable location of three reversals per session. Immediately following the completion of the 20 sessions of Phase 2, the rats were tested for an additional 10 sessions with three reversals per session. Using the same reversal locations as with one or two reversals per session (a reversal after Trial 10, 25, 40, 55, or 70), a total of 10 three-reversal session types were generated (see Table 1). The different session types were randomly assigned across sessions.

Results

Refresher Sessions

When the data were pooled over the last two sessions of the four refresher sessions, mean accuracy on Trials 36 to 45 with accuracy on Trial 41 omitted (the outcome of which was the first cue to reverse) was 90.3%. Thus, the rats' reversal accuracy on the refresher sessions was very similar to what it was at the end of Experiment 2a.

Phase 1

The percentage choice of the first correct stimulus as a function of relative trial number averaged over subjects for the last 10 sessions appears in Figure 3. As can be seen in the figure, subjects showed a significant improvement in performance from the feed-

Table 1
Different Combinations of Reversal Locations Within the Session for One, Two, and Three Reversals per Session

2 Reversal combos	S1 correct	S2 correct	3 Reversal combos	S1 correct	S2 correct	1 reversal/ session	S1 correct	S2 correct
10 & 25	65	15	10, 25, & 40	25	55	10	10	70
10 & 40	50	30	10, 25, & 55	40	40	10	10	70
10 & 55	35	45	10, 25, & 70	55	25	10	10	70
10 & 70	20	60	10, 40, & 55	25	55	25	25	55
25 & 40	65	15	10, 40, & 70	40	40	25	25	55
25 & 55	50	30	10, 55, & 70	25	55	25	25	55
25 & 70	35	45	25, 40, & 55	40	40	40	40	40
40 & 55	65	15	25, 40, & 70	55	25	40	40	40
40 & 70	50	30	25, 55, & 70	40	40	55	55	25
55 & 70	65	15	40, 55, & 70	55	25	70	70	10
Total	500	300	Total	400	400	Total	310	490
Percent overall	62.5	37.5	Percent overall	50	50	Percent overall	38.75	61.25

Note. For sessions in which two reversals occurred, the total possible combinations (10) resulted in a bias of S1 being correct 62.5% of the time. Therefore, in Phase 1 of Experiment 3, sessions with a single reversal were included among sessions with two reversals such that there were three sessions with a reversal after Trial 10 and Trial 25, two sessions with a reversal after Trial 40, and 1 session with a reversal after Trial 55 and Trial 70, making the overall number of trials with S1 correct approximately 50% (when combining the single and double reversal sessions). The combinations of reversal locations for three reversals are also shown. For sessions with three reversals, overall, there was an equal number of S1 and S2 correct trials.

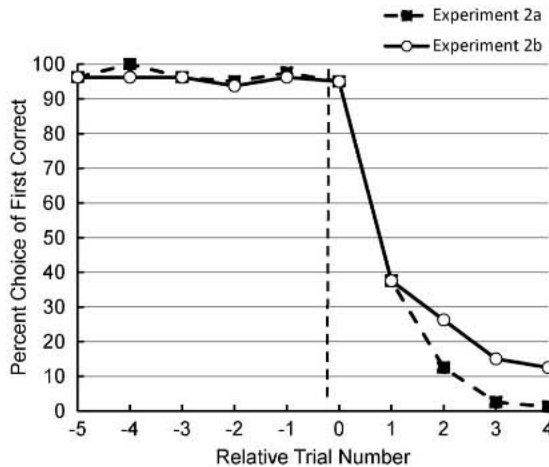


Figure 3. Experiment 2b; Phase 1. Percentage choice of the first correct stimulus (S1) as a function of relative trial number for the five trials prior to and after the reversal for the last 10 sessions of training (Sessions 5–15). The dotted line indicates the point at which the reversal occurred during the session. Data from Experiment 2a are shown as well for comparison purposes (closed circles).

back of the first reversal trial (mean $[M] = 95\%$ choice of S1) to the second reversal trial ($M = 38\%$ choice of S1), $t(7) = 15.71$, $p < .001$. For comparison, the data from Experiment 2a also appear in Figure 3. As can be seen, the rats showed little disruption of accuracy on the trial immediately following the reversal when the reversal could occur at a variable point in the session. However, on later trials following the reversal, there appeared to be some disruption of reversal accuracy. A correlated-samples t test revealed a significant difference between the percentage choice of S1 between Experiments 2a and 2b on the third, fourth, and fifth trials following the reversal, $t(7) = 3.27$, $p < .02$, $t(7) = 3.03$, $p < .03$, and $t(7) = 2.55$, $p < .04$, respectively.

Phase 2

The percentage choice of the first correct stimulus (S1) as a function of relative trial number averaged over subjects for all 20 sessions (10 sessions with the single variable reversal and 10 sessions with two reversals per session) appears in Figure 4. For sessions in which two reversals occurred, the first and second reversals of each of these sessions, averaged over subjects, are plotted separately. As can be seen in the figure, as expected, the single-reversal sessions and the first reversal during the two-reversal sessions show very similar functions. A correlated t test performed on the second trial of the reversal (sensitivity to the change in contingency) revealed no significant differences $t(7) = 1.72$, $p = .13$. However, the difference between the first and second reversal on the second trial of the reversal was significant, $t(7) = 2.73$, $p = .03$, suggesting that the second reversal was somewhat unexpected. However, accuracy on Trials 36 to 45, with accuracy on Trial 41 (the first cue to shift) omitted, was 87.9% for the first reversal and 81.5% for the second reversal in the session, a nonsignificant difference, $t(8) = 1.97$, $p = .08$.

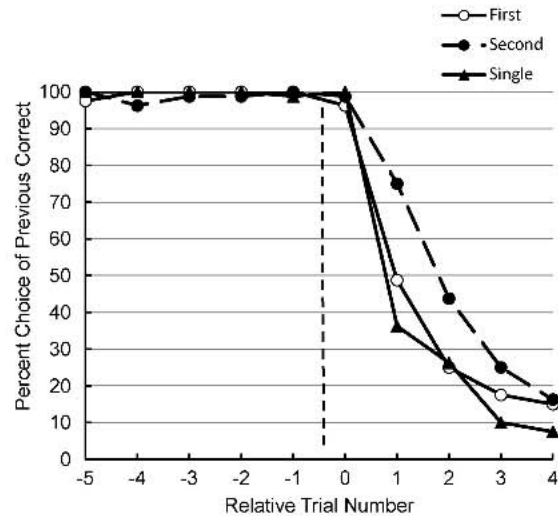


Figure 4. Experiment 2b; Phase 2. Percentage choice of the most recently correct stimulus as a function of relative trial number for the five trials prior to and after the reversal for the 20 testing sessions. The dotted line indicates the point at which the reversal occurred during the session. The graph depicts the choice of the most recent correct stimulus for the first reversal (open circles) and second reversal (closed circles) during the two-reversal sessions, as well as the sessions in which a single reversal occurred (closed triangles).

Phase 3

The percentage choice of the first correct stimulus as a function of relative trial number averaged over subjects for the 10 sessions with three reversals per session appears in Figure 5. Percentage choice of S1 on the first, second, and third reversals in each session

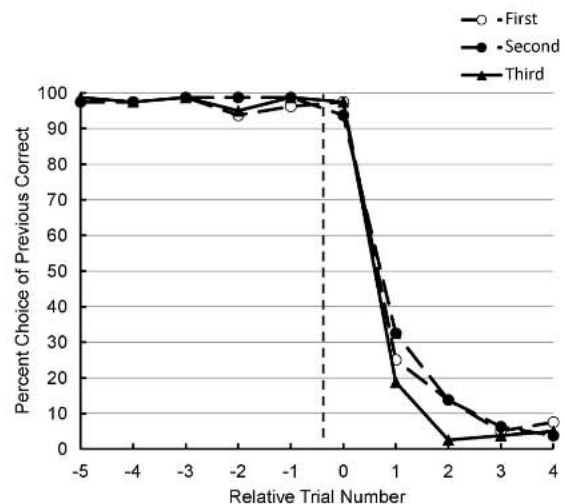


Figure 5. Experiment 2b; Phase 3. Percentage choice of the most recently correct stimulus as a function of relative trial number for the five trials prior to and after the reversal for the 10 testing sessions. The dotted line indicates the point at which the reversal occurred during the session. The graph depicts the choice of the most recent correct stimulus for the first reversal (open circles), second reversal (closed circles), and third reversal (closed triangles) during the three-reversal sessions.

are plotted separately. As can be seen in the figure, regardless of the location of the reversal, for the five trials prior to the reversal, the rats consistently chose the most recently correct stimulus (S1 for the first and third reversal and S2 for the second reversal). A correlated *t* test that assessed the sensitivity to the change in contingency as measured by the percentage choice of the most recently correct stimulus from the first to the second trial of the reversal was significant for all three reversals in the session. Choice of the previously correct alternative on the first and second trial of the reversal for the first reversal was 98% and 25%, $t(7) = 12.29, p < .0001$, for the second reversal was 94% and 33%, $t(7) = 7.35, p < .0001$, and for the third reversal was 98% and 19%, $t(7) = 10.97, p < .0001$. A one-way analysis of variance on the second trial of the reversal for each of the three reversal points revealed no significant difference in accuracy as a function of the reversal number (first, second, or third), $F(2, 24) = 2.87, p = .09$. Thus, once the rats had some experience with two reversals per session, they had no trouble adjusting to three reversals per session. Accuracy on Trials 36 to 45, with accuracy on Trial 41 omitted, was 87.2% for the first reversal, 86.0% for the second reversal, and 92.5% for the third reversal in the session. A one-way repeated measures analysis of variance performed on the accuracy on Trials 36–45, with accuracy on Trial 41 omitted, indicated that the differences were statistically significant, $F(2, 14) = 2.78, p < .05$.

Discussion

The results of Experiment 2b indicate that when one or more reversals could occur at variable points during a session, rats show very high accuracy prior to the contingency reversal, regardless of its location in the session, and they learn to rapidly adjust their responses to the newly reinforced stimulus after the change in contingency. In Phase 1, when the rats were initially exposed to the variable reversal location procedure, the differences in perseverative errors relative to those found in Experiment 2a were significant for the few trials following the reversal trial. This difference likely indicates that there was a small disruption in accuracy due to the change in procedure (the rats were given considerably more experience with the consistent as opposed to the variable reversal location). However, in Phases 2 and 3, in which multiple reversals per session were introduced, the rats showed almost no disruption in reversal accuracy with the additional reversals, and in fact, they showed the most accurate reversal performance during Phase 3 on the third reversal of the session. Overall, it appears that rats' ability to maximize reinforcement in Experiment 2a was likely due to the development of a rule-based strategy that is suggestive of a win-stay/lose-shift rule and was not a result of timing or trial-number estimation cues that could have been used and that pigeons appeared to use in Rayburn-Reeves et al. (2011) with a color discrimination reversal and in Experiment 1 of the present study with a spatial discrimination reversal.

General Discussion

Regardless of whether rats were tested with a single reversal at a consistent location, a variable point in the session, or multiple variable reversals, they showed a high level of sensitivity to the local feedback that allowed them to maximize reinforcement. This

result suggests that rats may be able to develop something very close to a win-stay/lose-shift rule. Such flexibility has been difficult to demonstrate in animals, and when demonstrated, generally requires a large amount of training (Warren, 1974). For example, in Harlow's (1949) research on learning set, monkeys were given a series of problems using simultaneous discriminations in which each discrimination problem involved a pair of novel stimulus objects. After given experience with hundreds of problems, the monkeys began to show win-stay/lose-shift performance such that their performance of the first trial of a new problem was at 50% and on the second trial rose to above 90%. Although the monkeys eventually acquired the win-stay/lose-shift rule, it took them hundreds of problems to reach that level. Similarly, serial reversal learning research has consistently shown that a variety of animals display progressive improvement over reversals (Beran et al., 2008; Bond, Kamil, & Balda, 2007; Gossette et al., 1966; Ploog & Williams, 2010; Warren, 1966) but rarely to the level at which accuracy on Trial 2 is above 90%, necessary to argue for the development of a win-stay/lose-shift rule (but see Dufort, Guttman, & Kimble, 1954; Staddon & Frank, 1974; Warren, 1965). Other research has shown that problem solving strategies may vary among subjects. Braggio, Braggio, Cochran, and Ellen (1983) showed that rats that acquired the original discrimination faster also tended to show better performance on Trial 2 as well as later trials of a reversal. They also made fewer errors defined as "win-shift" and "lose-stay," as compared with rats that acquired the original discrimination slower. The results of Braggio et al. (1983) suggest that the development of particular problem solving strategies may be evidenced in the rate at which the original discrimination is learned.

Traditionally, species differences in their ability to perform tasks such as these have been used to identify differences in their general level of intelligence (Bitterman, 1965). For example, under a variety of conditions, rats appear to be better prepared than pigeons to shift to an alternative not recently chosen. Specifically, rats have a natural tendency to spontaneously alternate (Still, 1966) and although they can easily learn a win-stay rule, research with the radial maze indicates that they also have a natural tendency to win-shift (Olton & Samuelson, 1976; Olton & Schlosberg, 1978; Timberlake & White, 1990). However, differences between rats and pigeons in the performance of this task may reflect differences in their natural foraging behavior. In terms of foraging ecology, rats do not often venture far from their nest; therefore, it is likely that the food that they find will appear in smaller patches. If they deplete those patches quickly, it would be adaptive for them to avoid returning to the depleted patch (win-shift). However, pigeons often travel much greater distances to a large patch (perhaps a field) where depletion is likely to take place slowly and it would be advantageous to return at a later time (win-stay). As opposed to rats, and consistent with this ecological interpretation, pigeons learn a radial maze analog task only with some difficulty and their natural tendency is to win-stay (Zentall, Steirn, & Jackson-Smith, 1990; see also Randall & Zentall, 1997). Similarly, in the present experiments, although rats learned to revisit a location associated with reinforcement (S1) and to reduce their tendency to sample the other alternative (S2) during training, they also quickly learned to shift to a different location with the change in reinforcement contingency and to continue to respond to S2 for the duration of the session. However, pigeons were not only less sensitive to the

changes in reinforcement contingency, but they made errors both prior to and after the reversal throughout training. Although these findings do not completely explain the differences between rats and pigeons found in the present series of experiments, they may suggest why rats are so much more efficient at switching to S2 in the midsession reversal task.

One possible account for the faster reversal by the rats than by the pigeons is that the rats had fewer exposures to the S- stimulus prior to reversal than the pigeons. Research has shown that repeated experience with the S- during overtraining (continued training on a discrimination after an animal reaches criterion) results in slower reversal learning performance (D'Amato & Jagoda, 1962) in rats. The fact that pigeons responded to the S2 (S-) stimulus more often than the rats prior to the reversal may have hindered their ability to inhibit responses to S1 (S-) when the contingencies reversed.

Similarly the saliency of the change in reinforcement conditions may have been greater for the rats than for the pigeons at the time of reversal. Rats averaged approximately 97% on the block of trials prior to the reversal, whereas the pigeons averaged approximately 70%. The lower percentage choice of the pigeons prior to the reversal means that they were receiving partial reinforcement, whereas the rat's performance more closely resembled continuous reinforcement. Research has shown that animals will extinguish responses to a previously reinforced stimulus faster if they have received continuous as opposed to partial reinforcement (Mowerer & Jones, 1945). According to the discrimination hypothesis (Erlebacher, 1963), the reason for this effect is that the change from continuous reinforcement to nonreinforcement (extinction) is more discriminable than a change from partial reinforcement to nonreinforcement. It has also been argued that animals trained on continuous reinforcement develop an expectation of reward and when reinforcement is withheld, the animal becomes frustrated (Amsel, 1962). According to Amsel, frustration should lead to variability in the response and that variability should increase the probability of choosing S2.

It is also possible that rats are more sensitive to frustration than pigeons. More sensitivity would mean that they would tend to make fewer anticipatory errors and thus they would experience more frustration at the point of the reversal. The fact that pigeons began responding to the S2 stimulus prior to the reversal may be an indication of a lesser amount of primary frustration that results in pigeons' performance declining prior to the reversal. The great sensitivity of the rats, then, to the feedback of previous outcomes might be due to the greater sensitivity to primary frustration that develops to the absence of reward in the presence of an expectation of the reward.

It may be that this reversal task can serve as a means of investigating the ability of animals to learn to use the feedback from reinforcement and the absence of reinforcement to respond to predictable changes in contingencies. Serial reversal procedures have the limitation of only providing evidence of differences on a quantitative level, as the only measure is the rate at which a reversal can be learned compared to original learning rates. Results using the midsession reversal procedure provide a more theoretically nuanced view of species flexibility. It indicates that pigeons appear to be unable to refrain from using time into the session as a cue even when more efficient reinforcement-based feedback cues are available, whereas rats are much more efficient in using those

feedback cues. These differences may indicate a fundamental difference in the type of information that can be used to solve the task between these two species and may further indicate a difference in the cognitive mechanisms available in mammals as opposed to avian species in solving this task. It would be of interest to determine if other avian species also have difficulty in using the feedback from the preceding trial as the basis for choice on the current trial and continue to use less efficient temporal cues with this task, as well as whether other mammals develop the more optimal choice behavior shown by rats. Thus, the midsession reversal task may be valuable procedure for testing differences in nonhuman animals and their ability to deal with a predictable change in contingency.

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