

Temporal discrimination in a long operant chamber

Armando Machado^{a,*}, Richard Keen^b

^a Instituto de Educação e Psicologia, Universidade do Minho, 4710 Braga, Portugal

^b Brown University, Providence, RI, USA

Abstract

Pigeons were placed in a long chamber equipped with one key and feeder at each end side and one key and houselight at the middle. To obtain food the birds had to choose one side key after a short signal and the other side key after a long signal. The signals consisted of the illumination of the center key and the houselight and were initiated by a peck at the center key. The chamber had sensitive floor panels that enabled us to measure the location of the bird during the signals. In Experiment 1, after the birds learned the discrimination we reversed the assignment of keys to signals. In Experiment 2, we examined performance on two pairs of discriminations holding the same ratio. In Experiment 3, after the pigeons learned to discriminate two signals, we changed the duration of the long signal. The results showed that (a) the birds' motion during the signal was highly stereotypical, i.e. the birds moved to the *short* side, waited a few seconds, and then departed to, and stayed on the *long* side; (b) this motion pattern predicted the results of generalization tests with novel durations; (c) the mean of the times of departure from the *short* side approached its steady state values quicker than the standard deviation and consequently superposition of behavioral measures became stronger with training; (d) only the duration of the short signal influenced significantly the moment the birds departed from the *short* side; finally (e) the times of arrival at and departure from the *short* side were positively correlated, but the times of arrival and residence at the *short* side were negatively correlated.

© 2003 Elsevier Science B.V. All rights reserved.

Keywords: Acquisition of temporal discrimination; Pigeon; Point of Subjective Equality; Psychometric function; Superposition property; Temporal bisection task

1. Introduction

In a temporal bisection task, an animal is presented with one of two stimuli that differ only in duration. A light may be turned on for 4 s or for 16 s, for example. At the end of the stimulus, the animal chooses between two alternatives, say a Left and a Right key. If the animal chooses the Left key after the short signal, or the Right key after the long one, then it is rewarded. We refer to the correct choice following the short and long stimuli as *short* and *long* choices, respectively. After the animal learns the discrimination,

the experimenter introduces signals with new durations and records the alternative the animal chooses. Then by plotting the proportion of times the animal chooses *long* against the duration of the test stimuli, the experimenter obtains a temporal psychometric function. This function has three main properties (e.g. Church and Deluty, 1977; Gallistel, 1990; Platt and Davis, 1983; Richelle and Lejeune, 1980). First, in terms of shape it is a monotonic increasing, ogive-like function, which starts close to 0 at short durations and approaches 1 at long durations; (2) the Point of Subjective Equality or PSE, also referred to as the indifference or bisection point, is at the geometric mean of the two training stimuli; and (3) the functions obtained after training with pairs of stimuli that hold the

* Corresponding author.

E-mail address: armandom@iep.uminho.pt (A. Machado).

same ratio (e.g. lights with durations of 1 and 4 s, 2 and 8 s, or 4 and 16 s) superpose when plotted against *relative* stimulus duration. This last property expresses in the temporal bisection task the ubiquitous scalar property of animal timing (Gibbon, 1977, 1981).

The preceding properties of the temporal psychometric functions are logically independent. In particular, it is possible to have the PSE at the geometric mean without superposition and reciprocally, superposition without the PSE at the geometric mean (e.g. Machado, 1997; Machado and Keen, 1999). Hence, it is an open empirical question whether these two properties emerge, as it were, at the same time in the course of the discrimination training, or whether one emerges before the other. In a similar vein, it is an open empirical question whether the animal bisects the signals at the geometric mean from the very first session in which it gives evidence of having learned the discrimination, or whether the bisection at the geometric mean occurs only after extended training. The same question can be raised about the superposition property: Is it the case that the psychometric functions superpose from the very first moment the animal's choices are above chance levels or only after prolonged training?

Unfortunately the standard bisection task is poorly suited to address these and similar questions concerning the acquisition of a temporal discrimination. For typically in this task the generalization tests occur only after choice performance following the two signals has reached a steady state, which means that information concerning the PSE or the potential superposition of the psychometric functions is not available until the end of acquisition. Moreover, the PSE itself must be interpolated from the psychometric function. The alternative that immediately suggests itself to address acquisition issues—to include generalization tests from the beginning of training—is not only cumbersome to implement but likely to change the very nature of the bisection task.

In the present paper, we report an alternative task—and some preliminary results obtained with it—that retains the advantages of the standard bisection procedure while enabling the experimenter to address acquisition issues. The key features of the task are the large separation between the two choice alternatives and the tracking of the animal's motions during the signals. Consider then a long chamber for pigeons equipped with two keys and feeders in opposite walls and sensi-

tive floor panels. To initiate a trial, the bird is required to peck a third key located in the middle of the chamber. As in the standard procedure, after the short or long signals, the two side keys are illuminated and if the pigeon chooses the correct side key it receives a reward through the feeder located below that key. As the animal learns the task, we expect that its motions during the signals will become increasingly differentiated and stereotyped. Specifically, we expect that at signal onset the animal will move towards the *short* side and remain there for at least the duration of the short signal; if the sample is the short signal, then the animal will be near the *short* key at the end of the trial, peck it, and receive the reward with minimum delay. However, if the sample is the long signal, we expect that sometime after the short duration has elapsed the animal will move to the *long* side and remain there until the end of the trial. At that moment the side keys will be illuminated, the animal will peck the *long* key and receive the reward, again with minimum delay.

During the *long* trials, a well-differentiated motion pattern may be characterized by three parameters, the time of arrival at the *short* side (Arrival), the time of departure from the *short* side (Departure), and the time of residence at the *short* side (Residence), where obviously Residence time equals Departure time minus Arrival time (for similar analyses see Gibbon and Church, 1992; Killeen and Fetterman, 1993). From the interrelation of these parameters, how they evolve with training, how they relate to the overall proportion of correct choices, and the like, the experimenter can address the acquisition questions identified before. Take for example, Departure time. The moment the bird leaves the *short* side may be considered a threshold-like criterion separating short signals from long ones. Durations below the criterion would be followed by choice of the *short* key, whereas durations above the criterion would be followed by choice of the *long* key. If this reasoning is correct, then the cumulative distribution of Departure times should match the proportion of choices of the *long* key obtained from the generalization trials. In other words, the cumulative distribution of Departure times should equal the traditional psychometric function; the mean Departure time should equal the PSE interpolated from the psychometric function; and the variability of the distribution of Departure times should equal the slope of the psychometric function. To summarize, provided the

task engenders well-differentiated displacement patterns during the sample stimuli, each session should yield the equivalent of a psychometric function.

The correlations between Arrival and Departure and Arrival and Residence times can also provide clues about the underlying processes of temporal regulation. Consider the following two examples. Animal A departs from the *short* side at approximately the same time since trial onset. Because early and late Arrivals are followed by Departures at approximately the same time, the correlation between Arrival and Departure will be 0. However, the correlation between Arrival and Residence will be negative because early Arrivals will be followed by longer Residences (i.e. the animal has to wait longer before reaching the Departure time), and late Arrivals will be followed by shorter Residences. As a second example, assume Animal B waits approximately a constant amount of time at the *short* side before Departure. In this case, the correlation between Arrival and Residence will be 0, whereas the correlation between Arrival and Departure will be positive.¹

In addition to the standard bisection procedure, the proposed task may be conceived also as a time–place learning task (for a review, see Roberts, 1998), for the animal has to learn where food is available when: Two distinct spatial locations—the end sides of the long operant chamber—have food available at two distinct moments—after the short and the long signals. The task is also analogous to Killeen and Fetterman's (1993) three-key peak choice procedure in which reinforcers were available from pecking the right key at 8 s into the trial, the center key at 16 s into the trial, or the left key at 32 s into the trial. In both tasks the birds have to learn to be at the right place at the right time. Finally the task is analogous to Catania's (1970) mixed Fixed Interval–Fixed Interval schedule. On a mixed FI 30-s–FI 240-s schedule, for example, a key peck is reinforced after a fixed interval of either 30 or 240 s have elapsed since trial onset; the two FI values are equally likely. If the experimenter assigns the two FI schedules to different keys, then the similarity

between the two tasks becomes apparent. The main difference between these other tasks and the task presented in this study is the large separation between the keys and the tracking of the animal's location during the sample stimulus.

In what follows we report three experiments using the new task. Experiments 1 and 2 asked whether the typical findings obtained with the standard bisection procedure occur also with the new task; in addition the experiments looked at the acquisition phase of the temporal discrimination. Some unexpected findings obtained during these experiments motivated Experiment 3, which asked a more specific question, 'What is the effect of changing the duration of the long signal in this temporal discrimination task?'

2. Experiment 1

In the first experiment pigeons were exposed to a 3 s- versus 12 s discrimination. We examined how the pattern of motion during the signals evolves across sessions and how its parameters relate to choice at the end of the trial. When performance reached a steady state we introduced generalization trials. Finally, we reversed the assignment of the choice keys to the training signals.

2.1. Materials and methods

2.1.1. Subjects

Four pigeons (*Columba livia*) maintained at approximately 80% of their free-feeding body weights participated in the experiment. They were housed in individual home cages with free access to water and grit. The pigeon colony was on a 12-h light on/12-h light off schedule. The pigeons were used in previous experiments unrelated to temporal discrimination.

2.1.2. Apparatus

The experimental box used in the experiment is drawn schematically in Fig. 1. All walls and ceiling were made of Plexiglas. The back wall was equipped with a circular response key, 2.54 cm in diameter, centered horizontally and 24.1 cm above the floor. The key could be illuminated with red or green light. The left and right walls were equipped with an identical response key—also 24.1 cm above the floor but 8 cm

¹ From the equality Residence = Departure–Arrival, the first case corresponds to a constant Departure time, say, d . Hence Correlation (Arrival, d) = 0, and Correlation (Arrival, d – Arrival) < 0. In the second case, Residence is constant, say, r ; hence Correlation (Arrival, r) = 0 and Correlation (Arrival, r + Arrival) > 0.

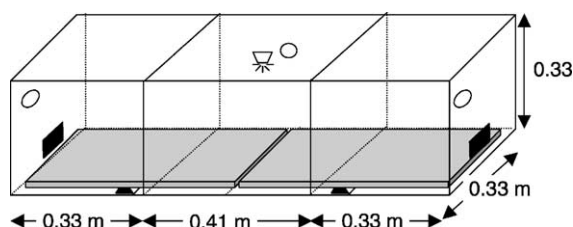


Fig. 1. Schematic of the operant chamber used during the experiments. Two switches were located underneath each floor panel.

off the horizontal center of the wall—and one feeder opening ($5.7 \text{ cm} \times 4.4 \text{ cm}$), centered horizontally and 5 cm above the floor. Two feeders, one behind each feeder opening, permitted access to grain when activated. The ceiling was equipped with a 24-V centrally located houselight. The animals were placed inside the box through a door located in the center of the front wall.

The floor of the box consisted of two rectangular wooden panels, placed side by side, each with a hinge in the middle and two switches underneath, one at each extremity. The hinges divided the box lengthwise into four segments, which we numbered as follows: 0 for the extreme left, 2 for the middle left, 4 for the middle right, and 6 for the extreme right. When the bird moved to one segment, the corresponding panel tilted and activated the switch at that location. When the animal stood on the middle of the box with one foot on each panel, the two innermost switches were activated simultaneously and the bird's position was assigned number 3. When the bird stood over the left hinge such that the left panel did not tilt, its position was assigned number 1 and, similarly, when it stood over the right hinge its position was assigned number 5. Thus, the numbers 0–6 indicated the bird's location in terms of its (approximate) distance to the extreme left end side of the box.

The box was placed on top of a table, 1 m above the floor, in a closed laboratory room. A 60-W lamp placed on a shelf behind and above the box provided general illumination and was always on while the experiment took place. All experimental events were controlled by a computer located in an adjacent room. In addition, a video camera, placed 50 cm away from the front wall and connected to a TV monitor in the adjacent room, allowed the experimenter to observe the bird during the session.

2.1.3. Procedure

After the birds learned to eat from both feeders they were shaped to peck the side keys when they were illuminated with red light. Afterwards the center key was illuminated with green light; a peck to this key turned it off and lit one of the side keys (randomly chosen) with red light; a peck at the illuminated side key activated the corresponding feeder for 2.5 s. After three to five sessions, all the birds reliably pecked the keys, ate from both feeders, and moved comfortably along the box.

During the experiment proper, each session was divided into trials and the following sequence of events characterized a *regular* trial (other types of trials are described below). The center key was illuminated with green light. A peck at that key changed its light to red and also turned on the houselight. The center key and the houselight remained illuminated for either 3 s, the short signal, or 12 s, the long signal. At the end of the signal duration, the center key and houselight were turned off and the side keys were illuminated with red light simultaneously. A peck at one of the side keys turned both of them off and if the peck was at the key associated with the signal then the feeder on that side was activated for 2.5 s; if the peck was at the other key, then no food was delivered. A 20-s intertrial interval (ITI) followed. During the ITI all keys and the houselight were off but the lamp located behind the experimental box remained illuminated. If the bird made an incorrect choice the next trial repeated the previous one (correction method), but after three consecutive errors only the correct side key was illuminated at the end of the signal. Throughout the trial the bird's horizontal location was determined by reading the floor switches once every 220 ms.

Besides regular trials, *extinction* and *generalization* trials occurred during the experiment. On extinction trials the choice response following the training signals was not reinforced, even if it was correct, and the correction method was not in effect. On generalization trials the signals differed in duration from the training signals, no reinforcer followed choice responses, and no correction method was in effect.

Phase 1: Initially, each session comprised 60 regular trials, 30 with the short and 30 with the long signal, randomly intermixed. The left key was the correct alternative following the short signal for three birds and following the long signal for one bird. After the

proportion of correct choices stabilized and at least 10 sessions were run (range: 12–16), the number of trials increased to 84, 60 of which were regular and 24 were extinction trials, 12 of each kind. After 5 sessions, the 24 extinction trials were replaced by 24 generalization trials with the following durations: 1.5, 4.2, 6.0, 8.5, 17, and 24 s. Together with the 3.0 and 12.0 training signals, these durations are elements of a geometric series with ratio 1.41; the middle duration, 6.0 s, is the geometric mean of the training signals. Each of the test durations occurred four times per session, randomly intermixed with the regular trials, and for a total of 10 sessions.

Phase 2: Immediately following the generalization sessions just described, the assignment of the side keys

was reversed such that the key that was correct after the short signal became correct after the long signal and vice-versa. Then the sequence of events followed during Phase 1 was repeated: 14 sessions with regular trials only were followed by 5 sessions with regular and extinction trials which in turn were followed by 10 sessions with regular and generalization trials. Bird 10405 became sick at the beginning of Phase 2 and therefore was removed from the experiment.

2.2. Results and discussion

The results that follow are based on the birds' behavior during the long trials, excluding correction trials. We consider four issues separately, how the birds

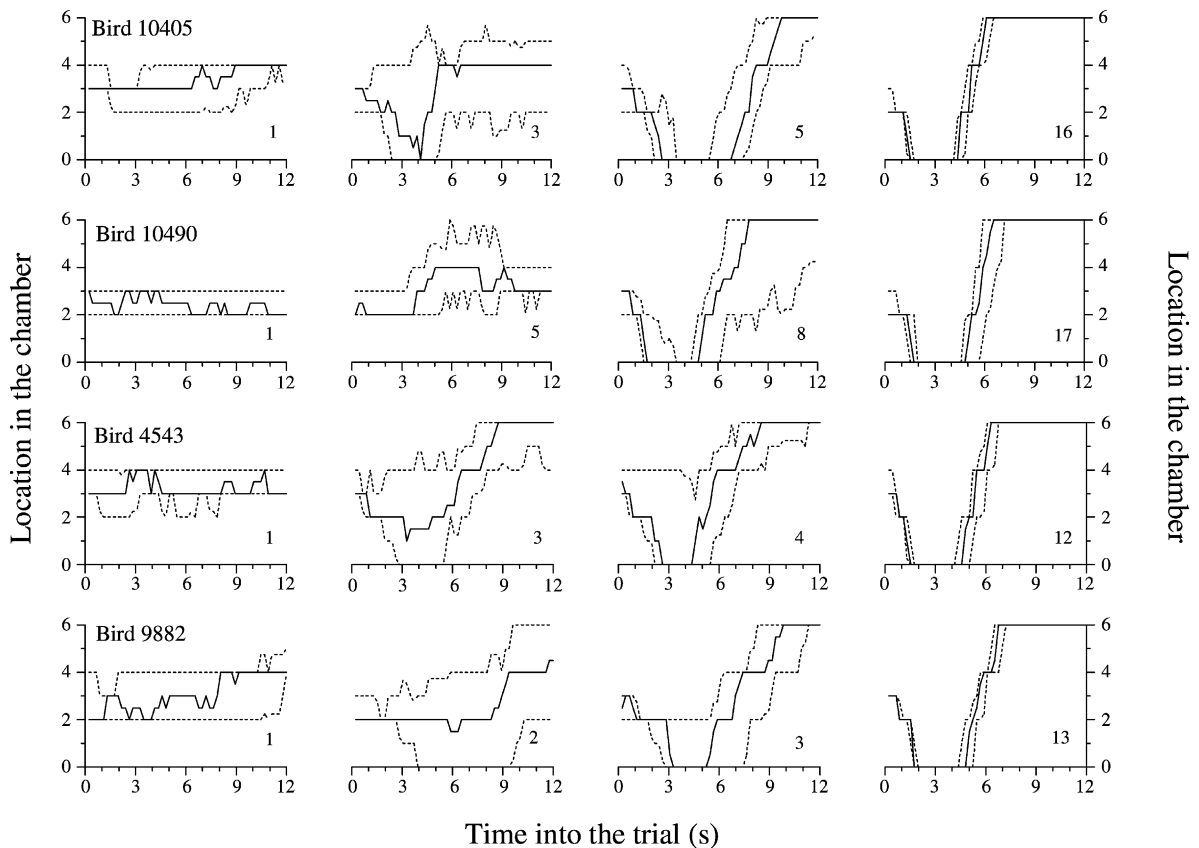


Fig. 2. Acquisition patterns obtained during Phase 1 of Experiment 1. The three lines are, from top to bottom, the upper, middle, and lower quartiles of the birds location during the long trials. The number in each panel identifies the session from which the data were obtained. The third panel from the left represents the first session in which choice proportion was significantly above chance following both short and long signals. The fourth panel represents the last session with regular trials only. Training signals were 3- and 12-s long.

learned the temporal discrimination, how their initial and terminal performances compare, how their location during the trial relates to the psychometric function, and how their times of Arrival, Departure, and Residence in the *short* side are inter-related.

2.3. Acquisition

Each panel of Fig. 2 displays the location of the bird at different moments into the trial. The panels on each row represent different sessions of the same bird. The solid lines show the median location and the lower and upper dotted lines show the first and third quartiles, respectively. In the first session, all birds stayed in the middle of the box during the trial, either pecking or orienting toward the center key. In the last session, all birds displayed a well-differentiated, highly stereotypical motion pattern: At trial onset, they moved to the *short* side where they arrived after 1.5 or 2 s; they stayed on the *short* side for approximately 2 or 3 s and then departed to the *long* side where they stayed until the end of the trial.

The two middle panels show the transition from clear absence to clear presence of the steady state mo-

tion pattern. In particular, the third panel from the left plots the data from the first session in which there was statistical evidence that the birds had learned the discrimination—i.e. for the first time the choice proportions following the short and the long signals were above the upper limit of the 95% confidence interval associated with random choice. The curves in these middle panels show the steady state pattern being assembled, as it were: The movement toward the *short* side at trial onset became stronger; the latency to arrive at the *short* side decreased; the duration of staying at the *short* side decreased and bracketed the 3-s moment with increasing frequency; and the duration of staying at the *long* side increased.

Fig. 3 shows the data for Phase 2. The pattern learned in Phase 1 persisted during the first session, particularly in Birds 10490 and 9882, but its mirror image was clearly visible during the final session. The curves in the two middle panels result to a large extent from mixtures of these two patterns. As in Fig. 2, the first session in which overall performance was significantly above chance already reveals the final pattern, although with higher variability (compare the two rightmost panels in Figs. 2 and 3).

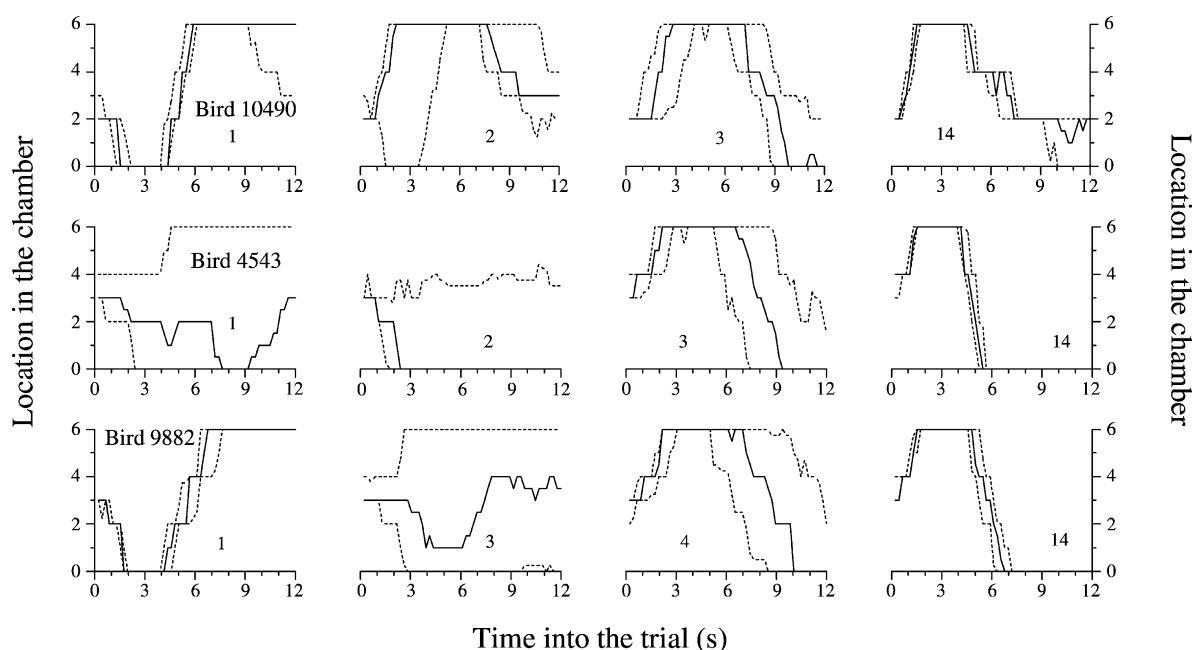


Fig. 3. Acquisition patterns obtained during Phase 2 of Experiment 1. Compared to Phase 1, the assignment of correct keys to signal durations was reversed. Training signals were 3- and 12-s long.

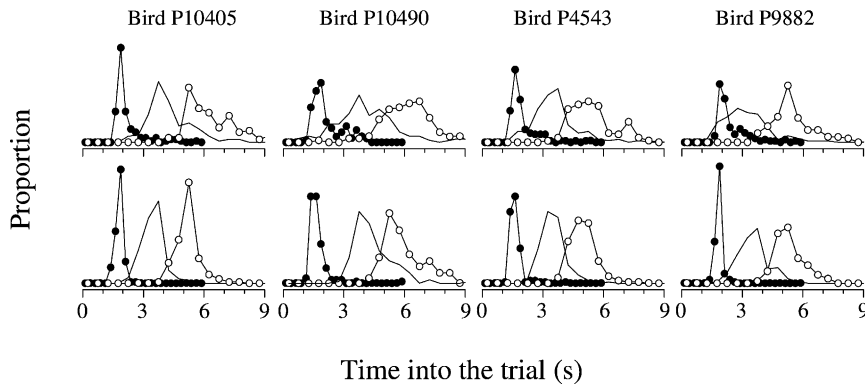


Fig. 4. Distributions of the times of Arrival at *short* side (filled circles), Departure from *short* side (empty circles) and Residence in *short* side during the first five (upper) and the last five (lower) sessions with regular trials only. Data from Experiment 1. Training signals were 3- and 12-s long.

2.4. Initial versus terminal performances

Fig. 4 shows the distributions of Arrival, Departure, and Residence times. These distributions were obtained from the trials in which the bird moved first to the *short* side and then to the *long* side. These trials always comprised more than 75% of all trials, and generally more than 90%. Concerning Phase 1, the averages of the Arrival and Departure times decreased with training for all birds, but only the changes in Arrival reached statistical significance ($t(3) = 9.4$, $P < 0.01$ for Arrival; $t(3) = 2.5$, $P = 0.09$ for Departure). The average of the Residence times did not change consistently across birds ($t(3) = 0.2$). For all birds and distributions, the standard deviation decreased appreciably with training: Arrival, $t(3) = 17.1$, $P < 0.001$; Departure, $t(3) = 7.6$, $P < 0.01$; Residence, $t(3) = 13.6$, $P < 0.001$. The corresponding distributions for Phase 2 yielded similar findings and are not shown.

Although both means and standard deviations changed with training, the changes in the standard deviations were far more substantial. For Arrival time the mean decreased from 14 to 28% across birds, but the standard deviation decreased from 36 to 70%. The corresponding changes for Departure time were 4–21% (mean) and 22–65% (standard deviation); for Residence time the mean changed across birds from an increase of 12% to a decrease of 20%, but the standard deviation always decreased (range 38–61%). We conclude that, once the birds learned the temporal discrimination, the effect of further training was mainly

to decrease the variability of Arrival, Departure, and Residence times.

2.5. Departure time and the psychometric function

As mentioned before, the moment the bird leaves the *short* side may be considered a criterion separating short signals from long ones. If this reasoning is correct, then the cumulative distribution of Departure times based on the regular trials should fit well the proportion of choices of the *long* key based on the generalization trials. Fig. 5 shows this was indeed the case for all birds and durations except in three cases, two involving the longest, 24-s stimulus (Bird 10405, Phase 1 and Bird 4543, Phase 2) and one the shortest, 1.5-s stimulus (Bird 9882, Phase 2). The PSE, estimated from the choice data by linear interpolation, was always below 6.0 s, the geometric mean of the two training signals (range: 3.9–5.4 s; overall mean: 4.7 s). The absolute differences between mean Departure time and the PSE estimated from choice data ranged from 0.1 to 0.5 s in Phase 1 and from 0.1 to 1.2 s in Phase 2. We conclude that the cumulative distribution of Departure times is a good approximation to the psychometric function and the mean of the Departure times a good approximation to the PSE.

Using the distributions of Departure times as equivalent to the psychometric function, we can answer one of the questions asked in Section 1, namely, how the psychometric function and the PSE change with training. From the first to the last sessions of training,

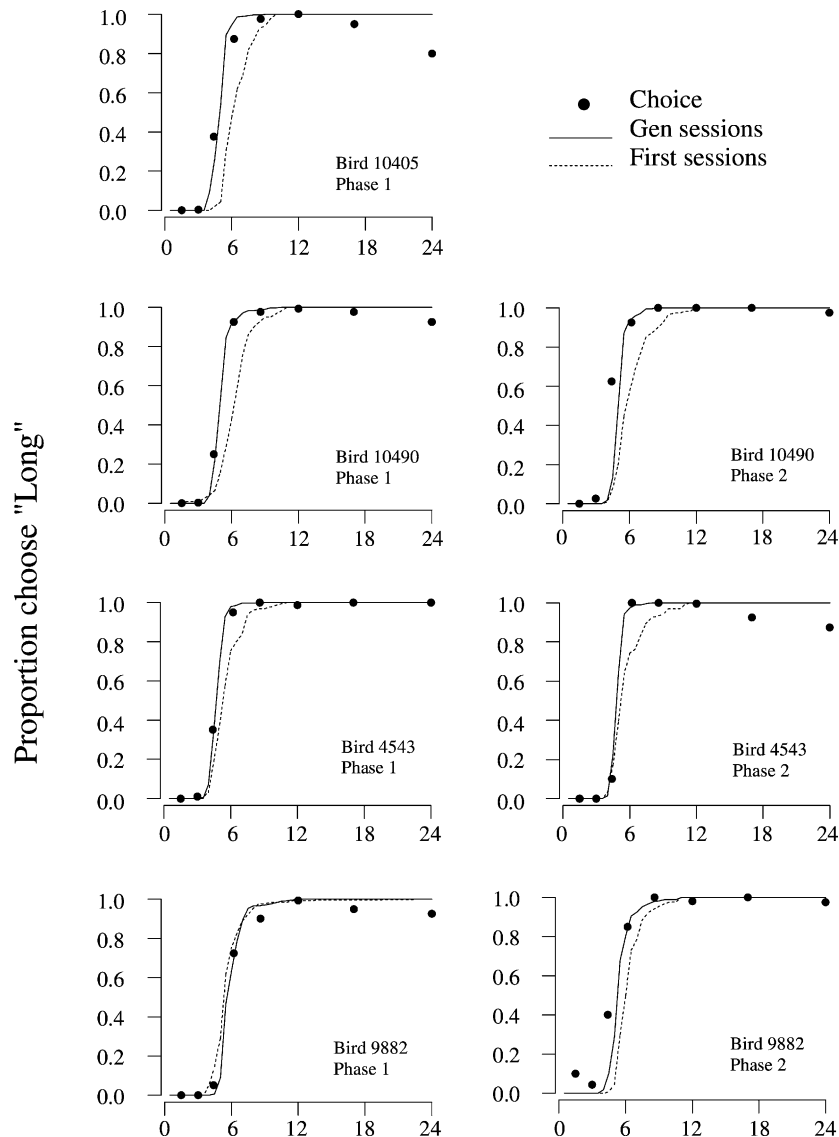


Fig. 5. The symbols show the choice proportions obtained during the generalization trials of Phases 1 (left) and 2 (right). The curves show the cumulative distributions of Departure times obtained from the regular trials of the first five sessions in which performance was above chance (dotted lines) and the last five sessions of training (solid lines). Training signals were 3- and 12-s long; their geometric mean is at 6.0 s.

the distributions shifted slightly to the left and became steeper for all birds and phases except Bird 9882 (Phase 1). This result is illustrated by the dotted lines in Fig. 5, which represent the cumulative distribution of Departure times based on the first five sessions in which choice performance was above chance. Interestingly, the means of these distributions were closer

to the geometric mean of the training stimuli than the means of distributions obtained later in training.

2.6. Correlation patterns

Having identified the first session in which there was evidence the birds had learned the temporal

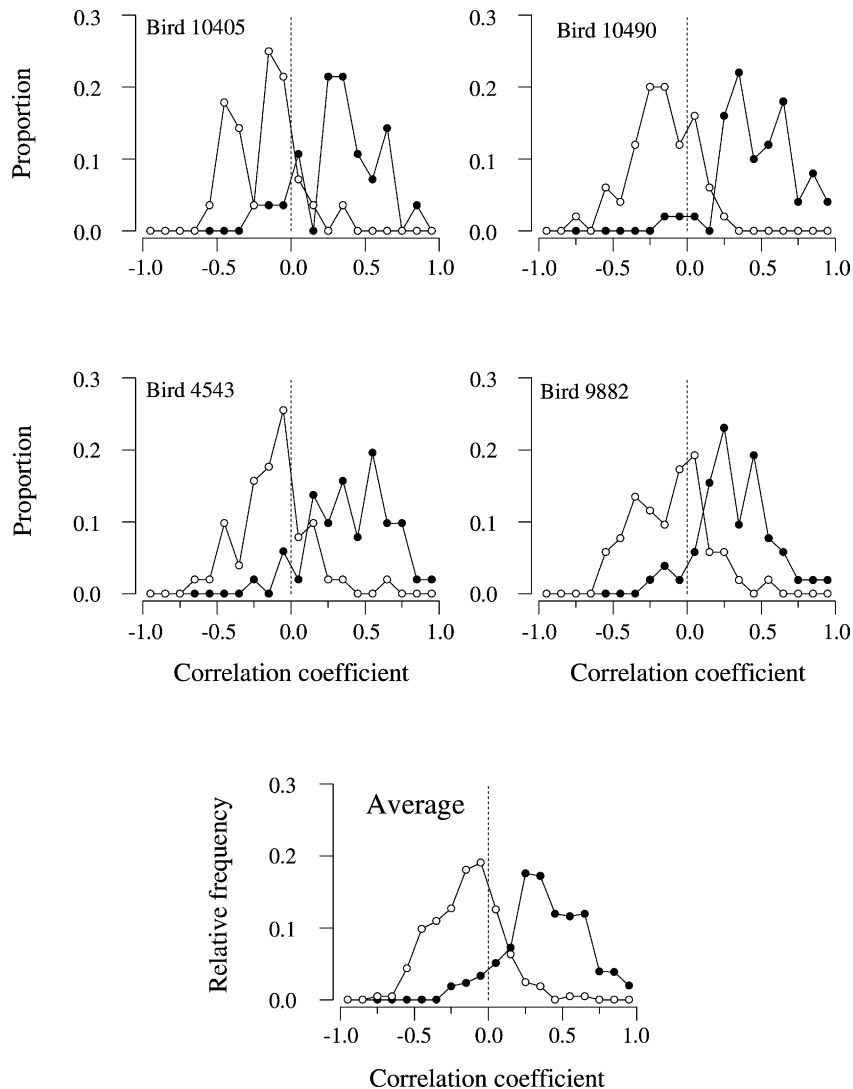


Fig. 6. Distribution of coefficients of correlation between Arrival and Departure times (filled circles) and Arrival and Residence times (empty circles). The data are based on all sessions of Experiment 1 except the (initial) sessions in which choice performance was below chance.

discrimination, we then computed two correlation coefficients for each subsequent session, the correlation between Arrival and Departure times, and the correlation between Arrival and Residence times. Next we plotted the distribution of the two correlation coefficients for each bird, and because Phases 1 and 2 yielded similar findings, we combined their data (except for Bird 10405). Fig. 6 shows the results. The correlation between Arrival and Departure times was generally positive and its average ranged across birds

from 0.32 to 0.47; the correlation between Arrival and Residence times was generally negative and its average ranged across birds from -0.18 to -0.11 .

In summary, as the proportion of correct choices increased, the birds' motion patterns became increasingly differentiated and stereotyped. From the moment there was evidence the birds had learned the task, mean Arrival, Departure, and Residence times were close to their steady state values, but their variability was greater than at the steady state. The Departure

times during the trial predicted well the bird's choices at the end of the trial, particularly when the sample duration fell between the two training durations. The initial mean Departure times were close to the geometric mean of the training stimuli but the final mean Departure times, as well as the PSEs estimated directly from the psychometric functions, were significantly below it. The Arrival and Departure times were moderately positively correlated, whereas the Arrival and Residence times were weakly negatively correlated.

3. Experiment 2

Assume a pigeon has learned to discriminate a 3-s signal from a 9-s signal and subsequently learns to discriminate a 9-s signal from a 27-s signal. The question asked in Experiment 2 was whether the bird's performance during the '9 vs. 27' condition was simply a scale transform of its performance during the '3 vs. 9' condition. Whether, in other words, the motion patterns and psychometric functions superpose when plotted in relative time.

3.1. Materials and methods

3.1.1. Subjects and apparatus

Four pigeons used in previous studies unrelated to temporal discrimination participated in the experiment. The housing conditions and the experimental apparatus remained as in Experiment 1.

3.1.2. Procedure

The training was in all respects equal to Experiment 1 except for the training durations. During the first phase of Experiment 2, the training stimuli were 3 and 9 s for two birds, and 9 and 27 s for the other two birds. During the second phase of the experiment, the training signals changed to 9 and 27 s for the first two birds, and to 3 and 9 s for the remaining two. Within each phase, 12–20 sessions with only regular trials were followed by 5–6 sessions with regular plus extinction trials and finally by 6 sessions with regular plus generalization trials. The number of regular trials per session equaled 60, evenly split between the short and long signals; the number of extinction trials per session equaled 24, also evenly split between the two training durations; and the number of generaliza-

tion trials equaled 25. When the training stimuli were 3 and 9 s, the generalization trials included the following signal durations, each presented five times per session: 1.73, 3.95, 5.20, 6.84, and 15.59 s. Together with the training signals, these durations are elements of a geometric series with ratio 1.32; the 5.20 value is the geometric mean of the training signals. When the training stimuli were 9 and 27 s, the generalization trials were three times as long: 5.19, 11.85, 15.60, 20.52, and 46.77 s.

3.2. Results and discussion

3.2.1. Acquisition

Fig. 7 shows acquisition data. During the first session of training, the birds stayed near the center of the chamber for the entire duration of the trial (see first panel from left). When proportion correct was above chance for the first time (second panel), the birds' motion patterns were reasonably well-differentiated but more variable than during the last session of training (third panel). These findings reproduce the results obtained in Experiment 1.

The two rightmost panels of Fig. 7 show that the motion patterns emitted during the last sessions of Phases 1 and 2 were similar: On most trials, the birds arrived at the *short* side before, and left that side after, the short duration elapsed. However, when the training durations changed across phases, (a) the Arrival times did not change systematically, for regardless of whether the short signal lasted for 3 or 9 s the birds tended to arrive at the *short* side 1 or 2 s after trial onset; but (b) the Departure times changed significantly and systematically, for when the training signals lasted for 9 and 27 s the Departure times were roughly three times longer than when the training signals lasted for 3 and 9 s.

3.2.2. Arrival, Departure and Residence times

Figs. 8 and 9 show distributions computed from the trials in which the bird moved first to the *short* side and then to the *long* side of the chamber. On the average, these trials comprised 90% of all trials. The absence of systematic changes in Arrival mentioned before is further illustrated in Fig. 8. The ratio of the means of the two distributions varied from 0.9 (Bird 1346) to 1.2 (Bird 4161) and the ratio of the standard deviations varied from 0.8 (Bird 1346) to 1.7 (Bird 4170). The

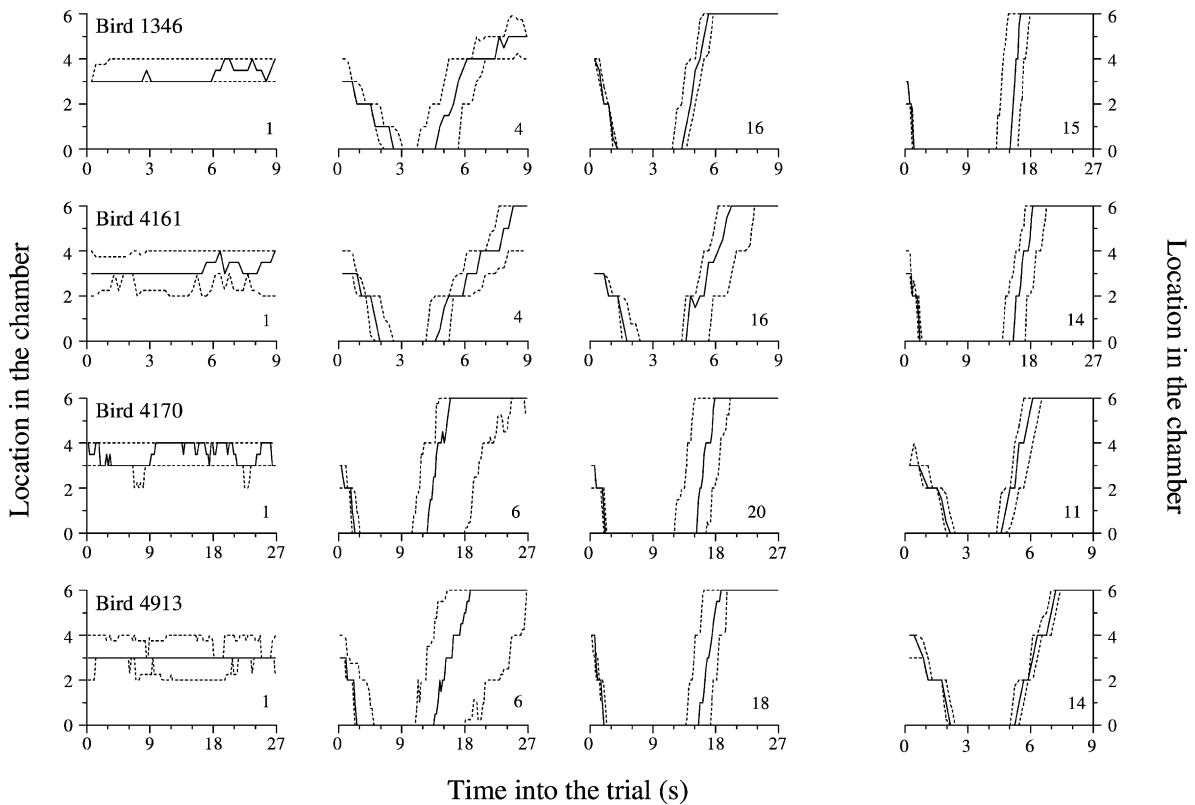


Fig. 7. The three leftmost panels in each row show the acquisition patterns obtained during Phase 1 of Experiment 2. The second panel represents the first session in which choice proportion was significantly above chance following both short and long signals. The third panel represent the last session with only regular trials. The rightmost panel shows the last session of Phase 2. Training signals were 3- and 9-s long, or 9- and 27-s long.

bottom panel shows that the average distributions from the two phases overlapped considerably.

Fig. 9 shows the distributions of Departure times. Plotted in *relative time*, the central tendencies roughly coincided, but in most cases the standard deviation was greater in the '9 vs. 27' than the '3 vs. 9' curves. This finding is expressed in the bottom panels by the greater width of the '9 vs. 27' average distributions. Although less clear in Fig. 9, it was also the case that the ratios of the standard deviations were closer to 1 when the sessions included generalization trials (right column, range of ratios: 1.0–1.2) than when the sessions included extinction trials (middle column, range of ratios: 1.3–1.9), the last sessions with regular trials only (left column, range of ratios: 1.0–2.2), or the first sessions in which performance was above chance (range of ratios: 1.0–1.9).

3.2.3. Departure times and the psychometric function

Fig. 10 shows the generalization choice data and the cumulative distribution of Departure times. Four findings are noteworthy. First, in most cases the curves fit the symbols well (the difference between mean Departure time and the PSE estimated by linear interpolation from the choice data averaged 0.4 s during the '3 vs. 9' condition and 0.6 s during the '9 vs. 27' condition). Second, the curves for the '3 vs. 9' discrimination are slightly steeper than the curves for the '9 vs. 27' discrimination, which is another expression of the proportionately larger standard deviations of the '9 vs. 27' distributions. Third, the two sets of symbols overlap considerably except for Bird 4170. And fourth, in four of the eight cases choice proportion at the geometric mean fell outside the 95% confidence interval

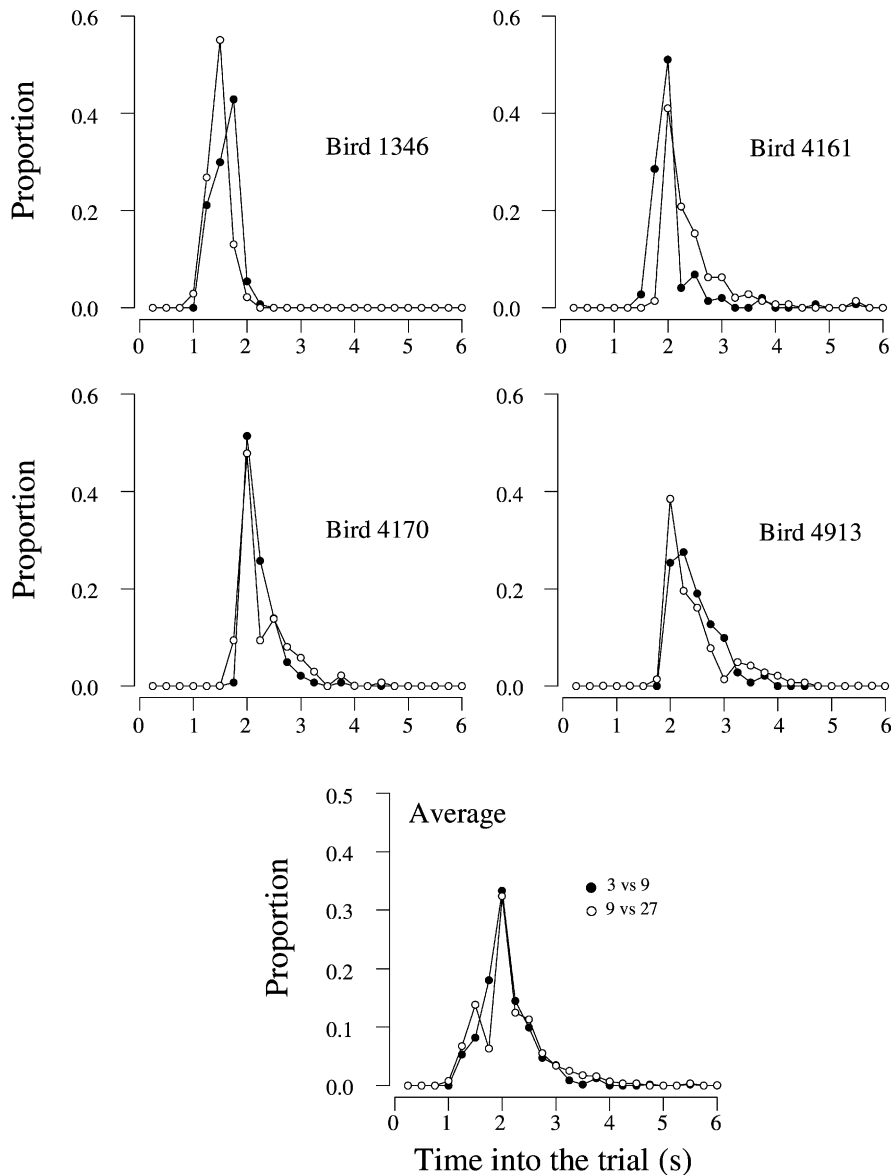


Fig. 8. Distributions of Arrival times during the '3 vs. 9' and the '9 vs. 27' discrimination in Experiment 2. Data from the last five sessions of Phases 1 and 2 which comprised regular trials only.

associated with indifference (normal approximation to the binomial).

The close fit between the cumulative distribution of Departure times and the psychometric function enables us to answer another question raised in [Section 1](#): Once choice performance is above chance, do the psychometric functions immediately superpose? For three

birds, the answer was negative, because the '9 vs. 27' curve (not shown) had a standard deviation more than three times greater than the '3 vs. 9' curve—the ratio of standard deviations equaled 4.0, 4.5, and 5.7; for the other bird (4161), the answer was positive, for the two curves overlapped considerably—the ratio of standard deviations equaled 2.9. Although the

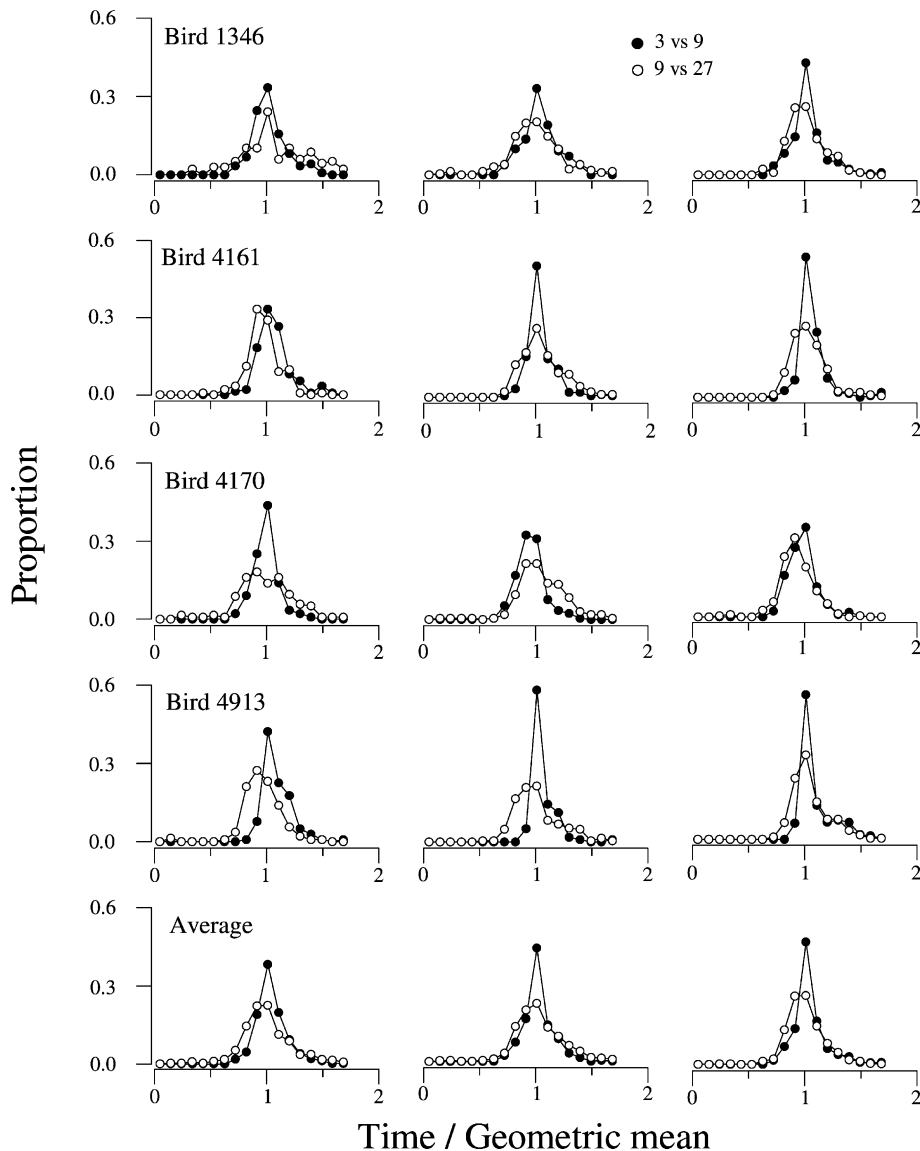


Fig. 9. Distributions of Departure times during the '3 vs. 9' and the '9 vs. 27' discrimination in Experiment 2. The data are plotted against relative time, with the geometric mean of the training signals as the standard. The left, middle, and right columns show the data from the regular trials of the last five sessions with regular trials only, regular plus extinction trials, and regular plus generalization trials, respectively.

data do not support a conclusive answer to the question, the changes in the Departure time distributions do support the following conclusions: (a) the mean and standard deviations of the Departure time distributions generally decrease with training; (b) the effect on the mean is weaker than the effect on the standard deviation; and (c) superposition becomes increasingly likely

with training. These conclusions were reached also in Experiment 1.

3.2.4. Inter-correlations

Fig. 11 shows the averages across birds of the distributions of the correlation coefficients. The average results are representative of the individual birds. The

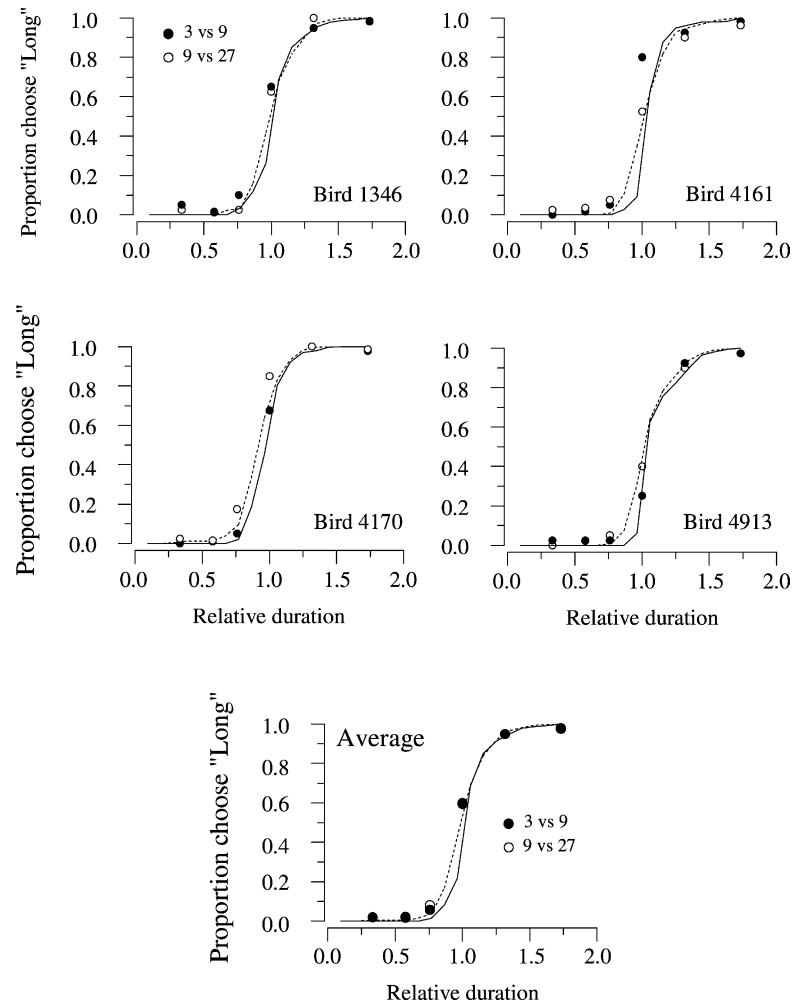


Fig. 10. The symbols show the choice proportions obtained during the generalization trials of the '3 vs. 9' and the '9 vs. 27' conditions in Experiment 2. The curves show the cumulative distributions of Departure times obtained from the regular trials of the last five sessions of training. The data are plotted against relative time, with the geometric mean of the training signals as the standard.

correlations between Arrival and Departure times were generally positive and the average ranged across birds from 0.03 to 0.29 when the training stimuli equaled 3 and 9 s, and from 0.15 to 0.44 when they equaled 9 and 27 s. In contrast, the correlation between Arrival and Residence times was generally negative and its average ranged across birds from -0.08 to -0.16 when the training stimuli equaled 3 and 9 s, and from -0.02 to -0.20 when they equaled 9 and 27 s. These results are consistent with the results of Experiment 1.

In summary, as the proportion of correct choices increased, the birds' motion patterns became increas-

ingly differentiated, a finding observed also in Experiment 1. When the training signals varied threefold across phases, the mean of the Arrival times did not vary systematically but the mean of the Departure times varied threefold. As a consequence, the mean of the Residence times changed more than threefold. In most cases the standard deviation of the Departure times varied more than threefold and it was only during the last conditions of each phase (i.e. during the sessions with regular plus generalization trials) that they approached the expected, three-fold change. Also as in Experiment 1, the Arrival and Departure times

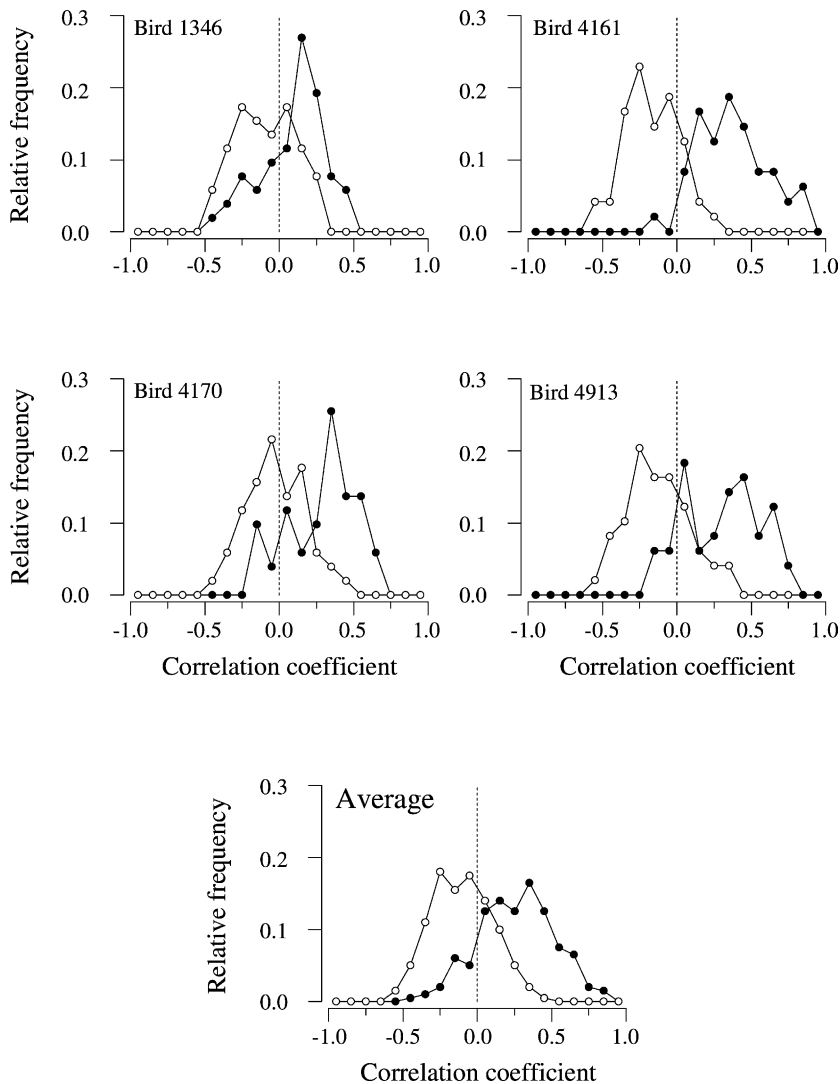


Fig. 11. Average distributions of the coefficients of correlation between Arrival and Departure times (filled circles) and the Arrival and Residence times (empty circles). The data are based on all sessions of Experiment 2 except the (initial) sessions in which choice performance was below chance.

were moderately positively correlated, whereas the Arrival and Residence times were weakly negatively correlated.

4. Experiment 3

When the training signals equaled 3 and 9 s in Experiment 2, the PSE's averaged 5.1 s and ranged across birds from 4.7 to 5.8 s. These values are similar to,

but slightly greater than, the values obtained in Experiment 1 in which the training signals equaled 3 and 12 s (mean 4.7, range: 4.0–5.0). If the PSE were at the geometric mean of the training signals, one would have expected slightly greater PSE's in Experiment 1 (geometric mean equaled 6.0 s) than in Experiment 2 (geometric mean equaled 5.2 s), the opposite of the observed trend. This finding, coupled with the finding that in Experiment 2 the Arrival times did not change systematically across phases but the Departure times

Table 1
Phases and conditions of Experiment 3

Bird	Phase 1						Phase 2									
	Condition 1			Condition 2			Condition 1					Condition 2				
	<i>S</i>	<i>L</i>	<i>N_R</i>	<i>S</i>	<i>L</i>	<i>N_R</i>	<i>S</i>	<i>L</i>	<i>N_R</i>	<i>N_E</i>	<i>N_G</i>	<i>S</i>	<i>L</i>	<i>N_R</i>	<i>N_E</i>	<i>N_G</i>
1309	3	27	20	3	9	11	9	81	15	5	10	9	27	11	5	7 ^a
2418	3	27	20	3	9	11	9	27	15	5	8	9	81	11	5	8
27033	3	9	20	3	27	12	9	81	15	5	8	9	27	10	5	8
488	3	9	20	3	27	12	9	27	15	5	8	9	81	10	5	9
2434	3	9	20	3	27	11	9	27	15	5	8	9	81	10	5	8

S and *L* are the short- and long-signal durations in seconds, respectively. *N* refers to the number of sessions with regular trials only (*N_R*), regular plus extinction trials (*N_E*), and regular plus generalization trials (*N_G*).

^a One session was lost.

did, suggests that only the duration of the short signal may have influenced significantly the birds' behavior. That is, the birds may have moved to the *short* side in a stereotypical way independent of the duration of the training signals—hence the absence of systematic changes in Arrival during Experiment 2. They then remained on that side an amount of time that depended on the short-signal duration—hence the similarity of the PSE's in Experiments 1 and 2, when the short signal equaled 3 s and the variation in Departure times across phases in Experiment 2. After that time had elapsed, the birds moved to the *long* side and remained there until the end of the trial.

If the foregoing interpretation is correct, then changing the duration of the long signal after the steady state has been reached should produce no effect. To illustrate, assume that after a bird learns a '3 vs. 9' discrimination, the experimenter changes the long signal to 27 s. If mean Departure time depends exclusively on the duration of the short signal, then it should not change. However, if mean Departure time depends on both signals and in particular if it coincides with their geometric mean, then it should change by a factor of 1.7, the square root of 3 (i.e. $(3 \times 27)^{1/2} / (3 \times 9)^{1/2} = 3^{1/2}$). Experiment 3 addressed this issue.

4.1. Materials and methods

4.1.1. Subjects and apparatus

Five pigeons used in previous studies unrelated to temporal discrimination participated in the experiment. The housing conditions and the experimental apparatus remained the same as in Experiments 1 and 2.

4.1.2. Procedure

Experiment 3 was divided into two phases. Within each phase the duration of the long stimulus varied while the duration of the short signal remained constant. Table 1 illustrates the details. In Phase 1, the short signal always equaled 3 s, whereas the long signal equaled either 9 or 27 s. During Phase 2, the short signal always equaled 9 s, whereas the long signal equaled either 27 or 81 s.

Based on the results of the preceding experiments, we predicted that the birds would acquire well-differentiated motion patterns during training, and these patterns would be strongly correlated with choice performance (cf. Figs. 5 and 10). Under these conditions, it would be redundant to include extinction or generalization test trials as we had done before. However, this prediction was confirmed only during Phase 1, for, as we describe below in greater detail, during Phase 2 the motion patterns became more variable across trials and birds. For this reason, we included extinction and generalization trials during Phase 2. The generalization trials comprised five durations, 3.0, 15.6, 46.8, 81.0, and 140.4 s when the training pair equaled 9 and 27 s, and 3.0, 15.6, 27.0, 46.8, and 140.4 s when the training pair equaled 9 and 81 s. These values correspond to elements of a geometric series with ratio 1.73. In all other respects Experiment 3 was identical to Experiments 1 and 2.

4.1.3. Results and discussion

Fig. 12 shows the median motion pattern, averaged across the last eight sessions of each condition of Phase 1. For most birds, the motion pattern during the long trials was well-differentiated and consistent with

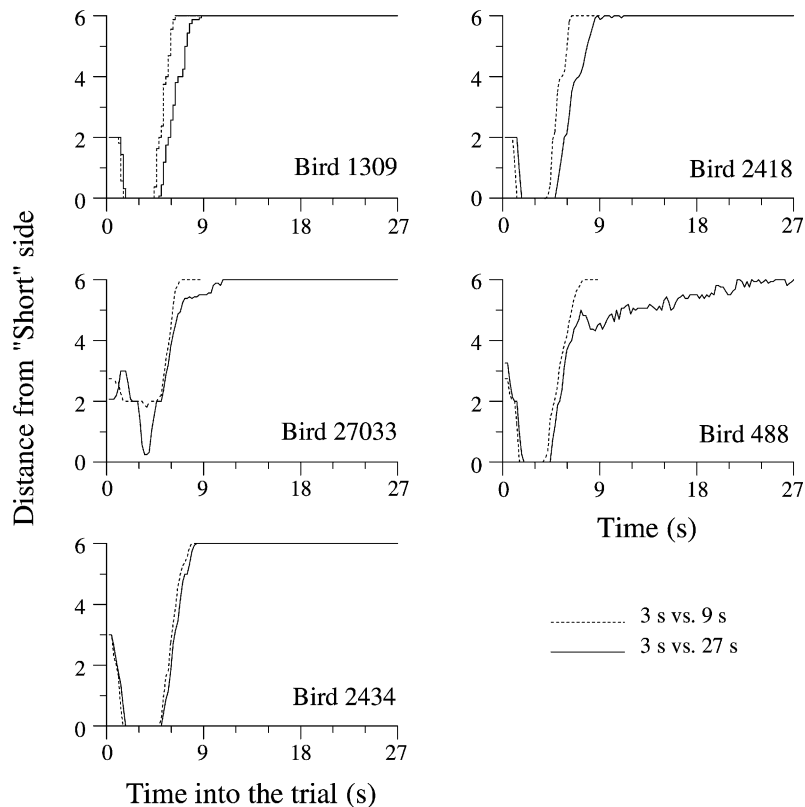


Fig. 12. Average of the median location curves obtained during the last eight sessions of Experiment 3, Phase 1, when the long signal equaled 9 s (dotted lines) or 27 s (solid lines).

the patterns observed in the preceding experiments. The exceptions were Bird 488—who in the ‘3 vs. 27’ condition moved back and forth along the chamber after departing from the *short* side—and Bird 27033—who tended to stay near the center of the chamber during the ‘3 vs. 9’ condition, and move back and forth along the chamber during the ‘3 vs. 27’ condition. Fig. 12 also shows that the three-fold change in the duration of the long signal had noticeable but small effects in three birds and no noticeable effects in two other birds. The fact that the clearest changes occurred in Birds 1309 and 2418 hints at a potential order effect, for these were the birds that experienced condition ‘3 vs. 27’ before condition ‘3 vs. 9’.

If we use the time each curve rises from 0 to 6 to estimate the PSE (or from about 2–6 in the case of Bird 27033), we obtain values in the range of 4.0–5.0 s during condition ‘3 vs. 9’, and in the range of 4.6–5.3 s during condition ‘3 vs. 27’. The former set of values is

close to, but slightly below, the geometric mean of the training stimuli. It is also consistent with the values obtained in condition ‘3 vs. 9’ of Experiment 2. The latter set of values, however, is substantially below 9.0 s, the geometric mean of 3 and 27 s.

Fig. 13 shows the distributions of Arrival, Departure, and Residence times. For all birds except 27033, the trials used to compute the distributions accounted for more than 90% of all trials; for Bird 27033 they accounted for 20% of all trials in condition ‘3 vs. 9’ and for 70% in condition ‘3 vs. 27’. Whereas for three birds there were small changes between conditions in the three types of distributions, for the other two birds the distributions basically overlapped. Again, the clearest changes were produced by the birds that experienced condition ‘3 vs. 27’ first, Birds 1309 and 2418. The means of the two distributions differed always by a factor substantially less than 1.7. In addition, the average across birds of the means of the Departure

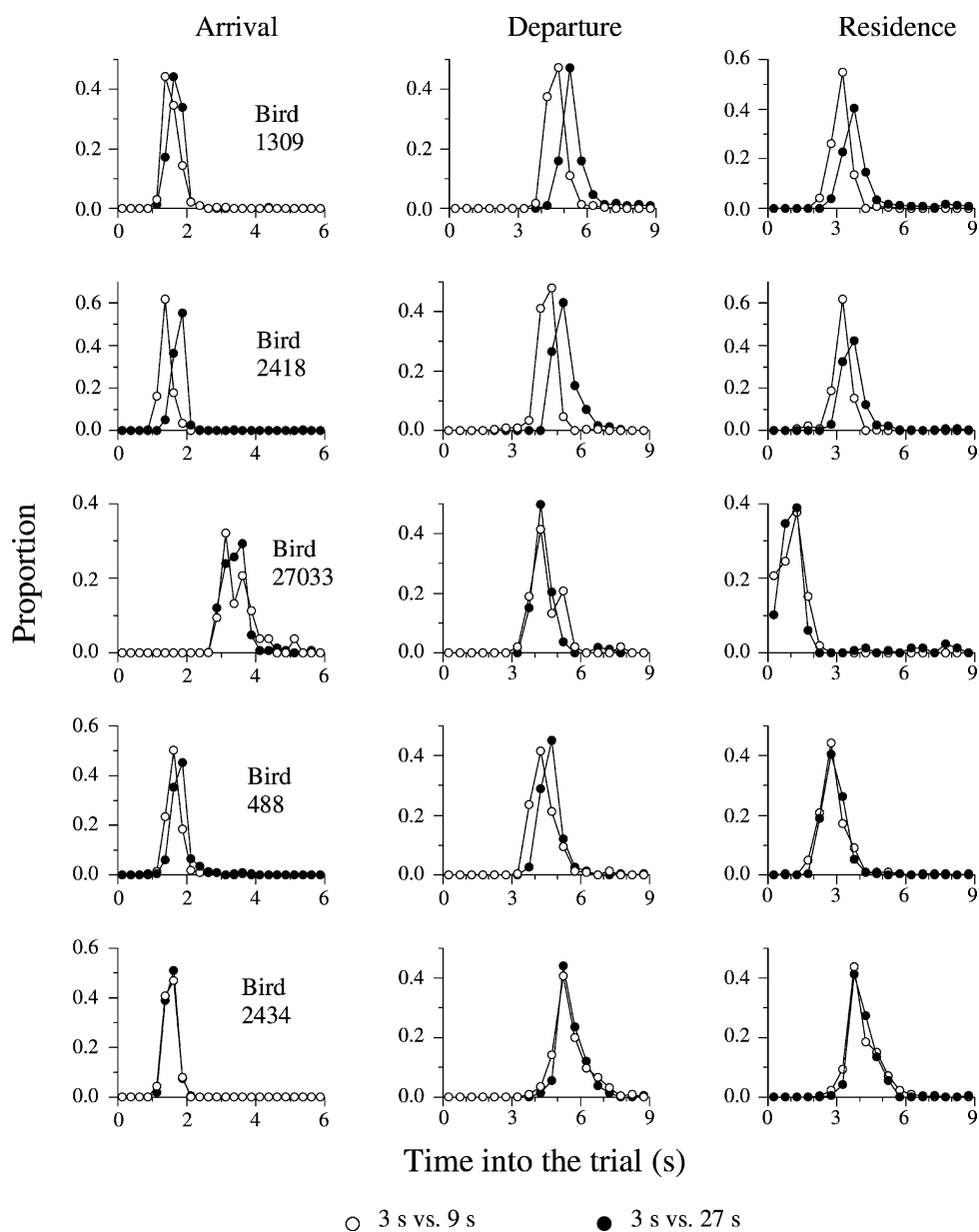


Fig. 13. Distributions of Arrival, Departure, and Residence times during the last eight sessions of Experiment 3, Phase 1. The long signal equaled 9 s (empty circles) or 27 s (filled circles).

distributions equaled 4.7 s during condition '3 vs. 9' and 5.6 s during condition '3 vs. 27'. The former average is close to, but slightly below the geometric mean of 5.2 s, but the latter average is substantially below the geometric mean of 9.0 s. The results based on the

three types of distributions are thus consistent with the results based on average motion patterns.

Figs. 14 and 15 show the data from Phase 2. The average motion patterns during Phase 2 became more variable across trials and birds, mainly because the

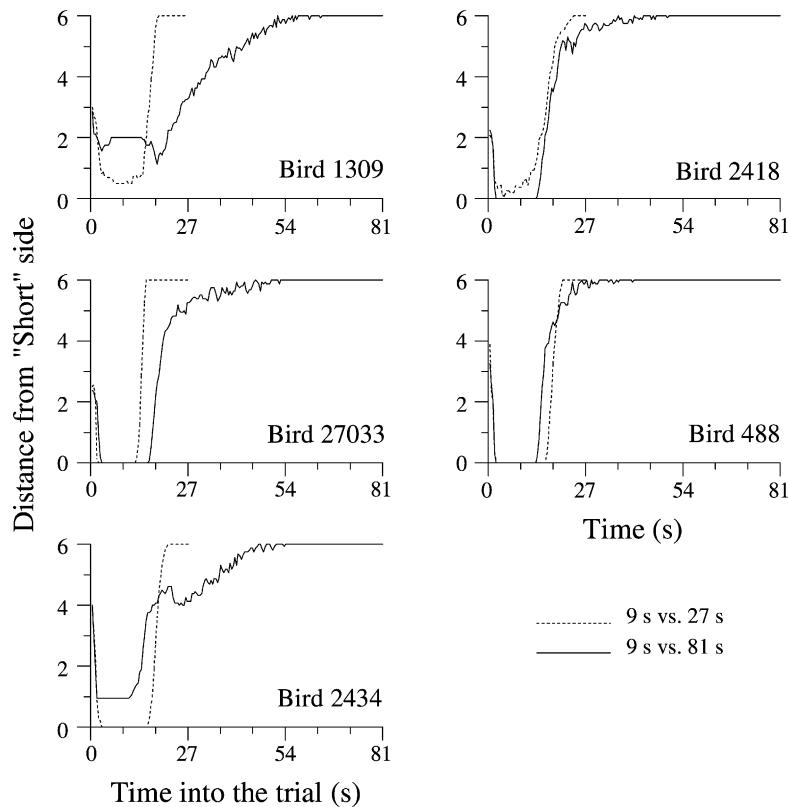


Fig. 14. Average of the median location curves obtained during the last eight sessions of Experiment 3, Phase 2, when the long signal equaled 27 s (dotted lines) or 81 s (solid lines).

birds either did not move all the way to the *short* and *long* sides of the chamber or moved back and forth along the chamber. Despite this increased variability, the results were similar to those observed in Phase 1, for whereas the average motion pattern changed in one direction for three birds, it changed in the opposite direction for the other two birds. Interestingly, as in Phase 1, the clearest changes occurred in the two birds (1309 and 27033) that experienced condition '9 vs. 81' before condition '9 vs. 27'.

The distributions of Arrival, Departure, and Residence times displayed in Fig. 15 also reveal the absence of consistent changes across experimental conditions: For three birds, the Arrival distributions overlapped considerably, and for two birds the Departure distributions during condition '9 vs. 81' had lower mean values than during condition '9 vs. 27'.

Finally, Fig. 16 shows the choice data from the generalization trials and the fit provided by the cumula-

tive Departure time distributions. Within the 3–27 s range, the two sets of data points showed no systematic differences. For three birds, the data from condition '9 vs. 81' were slightly to the right of the data from condition '9 vs. 27', but for the other two birds no effect was found. The superposition of the average curves within the 3–27 s range reveals clearly the absence of any systematic changes in choice performance. The PSE's estimated by linear interpolation averaged 16.0 s (range: 12.8–18.4 s) in condition '9 vs. 27', a value close to the geometric mean of the training signals (15.6 s), and 18.0 s (range: 13.1–24 s) in condition '9 vs. 81', a value substantially below the geometric mean of the training signals (27.0 s). The difference between the two sets of PSE values was not statistically significant ($t(4) = -1.09$, $P = 0.33$). Within the range of the training stimuli for each condition, the Departure time distribution fit the choice data well.

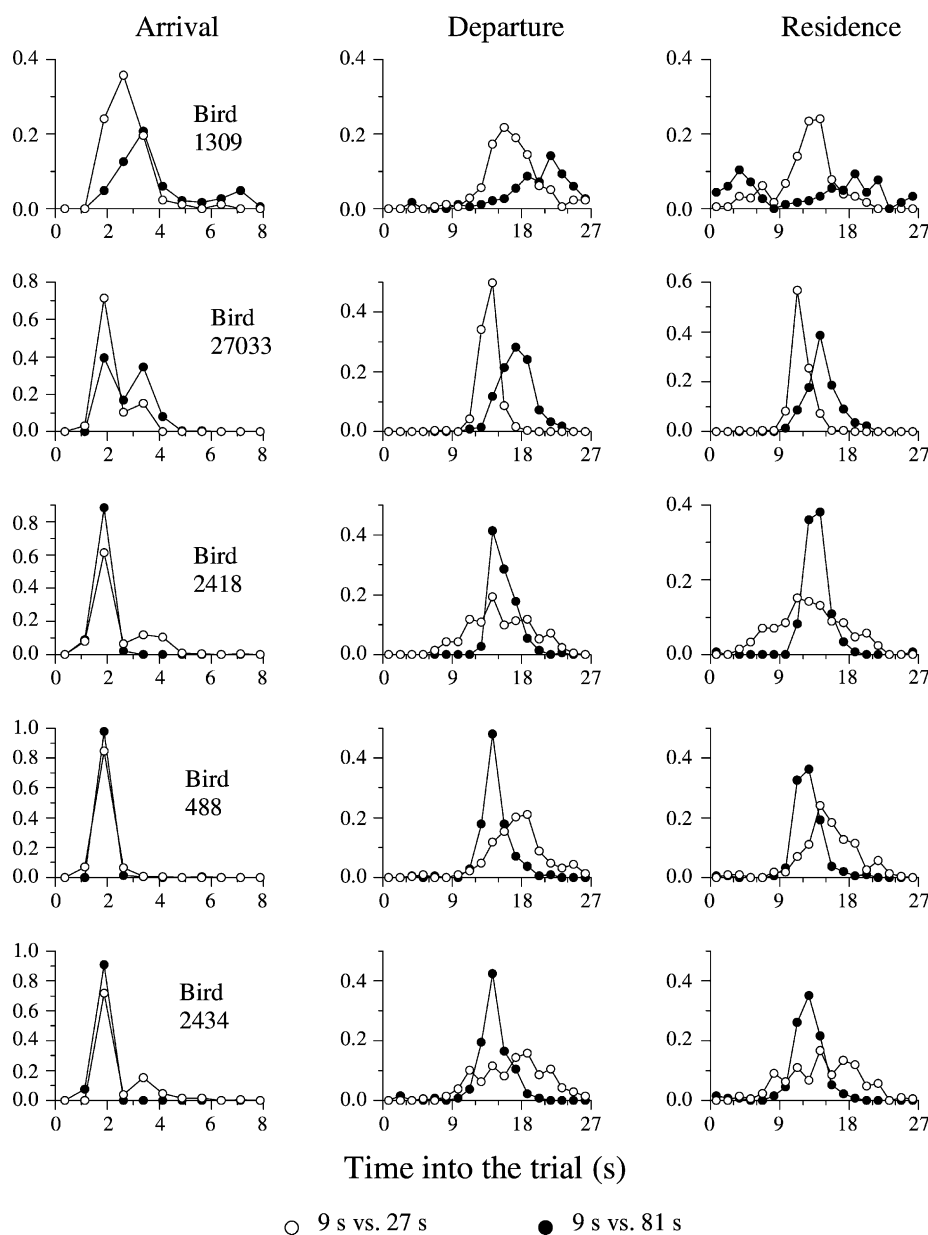


Fig. 15. Distributions of Arrival, Departure, and Residence times during the last eight sessions of Experiment 3, Phase 2. The long signal equaled 27 s (empty circles) or 81 s (filled circles).

But the two sets of data points differed outside the range of the training signals. In particular, during condition '9 vs. 27' the proportion of *long* choices following signals longer than 27 s was substantially reduced, a finding observed also in some birds during

Experiment 1 (see Fig. 5, Birds 10405 and 4543, Phase 2). The difference between the two sets of data at the longer signals reveals a clear effect of the duration of the long training signal. In other words, the long signal used during training did not affect systematically

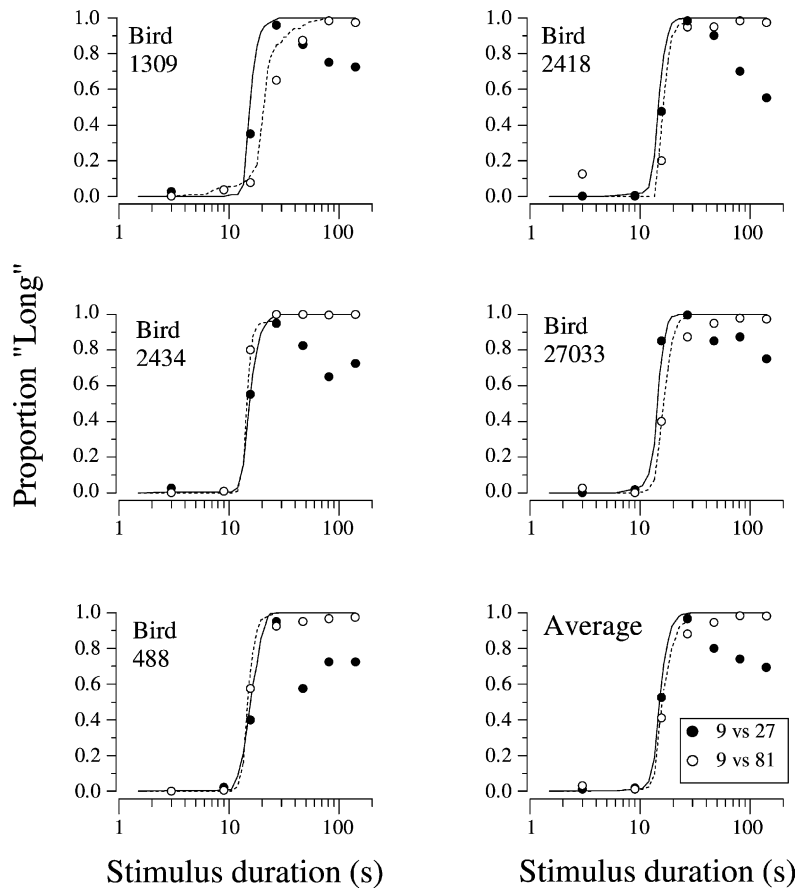


Fig. 16. The symbols show the choice proportions obtained during the generalization trials of Experiment 3, Phase 2, when the long signal equaled 27 s (filled circles) or 81 s (empty circles). The curves show the cumulative distributions of Departure times obtained from the regular trials of the last eight sessions of training. The data are plotted with logarithmic x -axes. The geometric means of the training signals were 15.6 s (long signal of 27 s) and 27 s (long signal of 81 s).

the times of Arrival to, and Departure from, the *short* side—and, a fortiori, the Residence time at that side—but affected the Residence time at the *long* side: After training with an 81-s signal the birds stayed at the *long* side longer than after training with a 27-s signal.

5. General discussion

The three experiments used a temporal discrimination task with choice alternatives far apart and a tracking system that records the location of the animal throughout the trial. Perhaps the greatest advantage of this task is that it enables the experimenter to examine the relation between the animal's behavior

during the trial and its performance at the end of the trial. It is well-known that pigeons, for example, often engage in idiosyncratic behaviors during the signal to be timed, behaviors that correlate well with their choices at the end of the signal (e.g. Machado and Keen, 1999; Richelle and Lejeune, 1980). According to some theoretical accounts such as Killeen and Fetterman's (1988) Behavioral theory of Timing (BeT) or Machado's (1997) Learning to Time model (LeT), these behaviors and their serial organization constitute the basis of temporal discrimination. But the topographies of these behaviors are hard to predict and difficult to measure. Replacing them by regular motions during the trial, that is, substituting displacements along the chamber for stretches of the neck or

head bobbings, improves the experiment both technically and conceptually; technically because location is easy to measure and correlate with choice, and conceptually because the temporal differentiation of the animal's motion during the trial—*when* it arrives at the *short* side, *how long* it resides on that side, and *when* it departs to the *long* side—manifests the underlying states assumed by BeT and LeT. Where the animal stands in the box expresses quite literally where it stands in time.

Furthermore, procedures in which the animal's location during the trial correlates strongly with choice at the end of the trial permit us to investigate a set of issues that would be difficult to investigate with other procedures in the traditional operant chamber: How do pigeons learn the discrimination? How do the mean and standard deviation of time estimates evolve with training? How early in training is the scalar property observed? In what follows we summarize the results related to these and similar questions, covering steady-state data first and acquisition data next.

5.1. Summary of steady-state data and two interpretations

In Experiments 1 and 2, we asked whether the usual properties of temporal discrimination—the ogive-like psychometric function, the bisection of the two intervals at their geometric mean, and the superposition of behavioral distributions when plotted in relative time—would be reproduced in the new task. In Experiment 3, we examined the effects of changing the long-duration signal. The results showed that with the exceptions discussed below the new task yielded the usual findings: The psychometric functions always had the standard ogive shape; in Experiments 1 and 2, the functions obtained with pairs of signals holding the same ratio overlapped considerably when plotted in relative time; and also in Experiments 1 and 2, the PSEs were close to the geometric mean of the training stimuli.

The exceptions were of two types. In Experiment 3, a three-fold change in the duration of the long signal did not affect the PSE consistently across birds nor were the differences between the PSEs statistically significant; some birds did change their PSEs but even in these cases the values of the new PSEs were substantially smaller than the geometric mean

of the new signals. The second exception was that in Experiment 1 the PSEs were always below 6.0 s, the geometric mean of the training stimuli. These two exceptions suggest that the PSE—and its close equivalent, the mean of Departure times—may have been influenced mainly by the duration of the short signal. Other evidence corroborates this conclusion, namely, in Experiment 2 the Arrival distributions did not change systematically after a three-fold change in the training stimuli. But we should not conclude that the long stimulus had no effect on performance, for the generalization tests of Experiment 3 clearly revealed that choices following markedly long signals varied orderly with the duration of the long training stimulus (see Fig. 16 and also Fig. 5, Bird 10405).

How should we account for the foregoing results, particularly (a) the small and statistically not significant change in the PSE when the long signal tripled in Experiment 3, (b) the absence of change in Arrival when the training signals varied, and (c) the occasional decrease in proportion of *long* choices when the test stimulus was much longer than the long duration stimulus? One possibility is as follows: At signal onset the birds moved to the *short* side in a stereotypical way such that the Arrival times did not depend on the signal durations—hence finding (b); then they waited on the *short* side an amount of time that depended mainly on the short duration—hence finding (a); then they departed to the *long* side and waited there an amount of time that depended on the long duration—hence finding (c). According to this account, changing the long stimulus duration does not affect the PSE significantly because the stereotypical motion pattern acquired before the change remains consistent with the new long-signal duration. To see this, consider the '3 vs. 9' discrimination in Experiment 3. A bird learns to move to the *short* side, wait there a few seconds, and then leave to the *long* side at about 5 s into the trial. When the long signal changes to 27 s, the pattern acquired during the previous condition remains adequate to deal with the new contingencies, adequate in the sense that it will not increase the number of errors and consequently decrease the number of reinforcers. However, when the short signal changes to 9 s, the old pattern engenders many reinforcer losses during the short trials (the bird leaves too soon), which losses are gradually eliminated as the bird learns to stay longer at the *short* side.

The preceding account is consistent with Platt and Davis' (1983) results. The authors found that in the standard bisection procedure the PSE depends on the two training durations only when the ratio of the short and long intervals is relatively small (e.g. 1:2 or 1:4), not when it is large (e.g. 1:8 or 1:16). In their Experiment 2, the short interval was held constant while the long interval varied. When the ratio was small, the PSE was close to the geometric mean (as measured independently by response rate and the median switch time), suggesting that both the short and long durations influenced the PSE, but when the ratio was large (1:8 or 1:16), the PSE was ambiguous: Looking at response rates yielded a PSE consistently below the geometric mean, whereas looking at the median switch time yielded a PSE consistently above the geometric mean. Platt and Davis concluded that (a) this ambiguity was a result of a period of low or no responding between the short and long values and (b) the pigeons treated the short and long signals independently in the sense that their responses before the period of no responding were solely affected by the short signal and their responses after the period of no responding were solely affected by the long signal.

The preceding account is also similar to Leak and Gibbon's (1995) interpretation of steady-state performance in mixed FI–FI schedules. Typically pigeons behave as follows during the long trials of a mixed FI–FI schedule: They pause at trial onset, then peck during an interval that brackets the duration of the short FI, then pause again (or peck at a lower rate), and finally peck until the end of the trial. Leak and Gibbon (1995) argued that the birds' behavior during the first part of the trial depends exclusively on the short-duration FI, whereas their behavior during the last part of the trial depends exclusively on the long-duration FI.

A second account of our findings is provided by Killeen et al.'s (1997) Pseudo Logistic Model. On the basis of Weber's law, these authors argued that the PSE may actually range from the harmonic to the geometric to the arithmetic mean according to the duration of the training signals and the dominant source of variability and error in a hypothetical pacemaker/counter system. For the range of durations used in the present experiments, the authors predict a PSE at the value $HM(L, S) \times [1 + w \ln(L/S)/2]$, where $HM(L, S)$ is the harmonic mean of the Long and Short training signals,

w is the Weber fraction, and \ln is the natural logarithm. To check this prediction we estimated w for each bird by dividing the standard deviation by the mean of its Departure times. The average of the predicted PSEs was close to the average of the obtained PSEs: Experiment 1, 5.3 versus 4.7; Experiment 2, 4.8 versus 5.1 when the discrimination was between 3 and 9 s, and 14.7 versus 15.1 when it was between 9 and 27 s; and Experiment 3, 15.0 versus 16.0 when the discrimination was between 9 and 27 s, and 18.6 and 18.0 when it was between 9 and 81 s.

The close match between the two sets of values shows that the Pseudo Logistic Model accounts for our PSE data without assuming that Departure time depends on both signals when their ratio is relatively small, but only on the short signal when their ratio is relative large. However, Killeen et al.'s model does not account for our remaining findings, particularly the downward trend of the psychometric function at very long test durations. Having conceived of the animal as choosing *long* whenever the percept corresponding to the signal is greater than a criterion threshold, the Pseudo Logistic Model predicts always a monotonic increasing psychometric function. In the end it is possible that both accounts are correct, for the Pseudo Logistic Model addresses only one aspect of the animal's behavior during the entire trial—how it decides to leave the *short* side—whereas our account describes the animal's entire behavioral pattern during the trial.

5.1.1. How did the birds learn the task?

The acquisition data (Figs. 2, 3, and 7) give a portrait of how the birds learned the temporal discrimination. Initially they stayed around the center key throughout the trial; later, they moved to the *short* side, waited there until the short-signal duration elapsed, moved to the *long* side and waited there until the end of the trial. The transition between the initial undifferentiated pattern and the final well-differentiated pattern may be characterized as putting together a set of behavioral segments. In fact our observations of the 'errors' made by the birds during the first sessions showed that they had to learn (a) to move to the *short* side at signal onset, (b) to stay at the *short* side until the short duration elapsed—too early a departure and the consequent choice of the *long* key meant the loss of the reinforcer on short trials; too long a stay and the consequent choice of the *short* key meant the loss of

the reinforcer on long trials; and finally (c) to stay at the *long* side until the end of the trial, for too short a stay on that side and the consequent choice of the *short* key meant the loss of the reinforcer on long trials. Variations of these behavioral segments early in training and their respective consequences (e.g. what we have called ‘errors’) help to explain properties of steady-state data (see Section 5.1.2).

Other aspects of the learning process were more subtle and did not reveal themselves in the acquisition curves. For example, initially the birds tended to choose whichever key they were facing at the moment of choice. A bird could be at the *long* side and yet, because it was facing the *short* side when the choice keys were illuminated, it tended to peck the *short* key. This bias was never completely eliminated and it may explain three sets of additional findings. First, some cumulative distributions of Departure times underestimated the proportion of *long* choices following short-signal durations and overestimated them following long-signal duration (e.g. Fig. 5, Bird 9882, Phase 2; Fig. 12, Bird 4161). This discrepancy may be due to the fact that before the bird departs to the *long* side it turns to face that side; if the keys are illuminated after the bird has turned but before it has started to move, then based on its location one would incorrectly predict the choice of the *short* key. Similarly, when the bird is at the *long* side, occasionally it may turn and face the *short* side; if the choice keys are illuminated at that time, the bird may peck the *short* key even though its location would predict a peck at the other key. Second, during some generalization trials with very long durations, the proportion of *long* choices decreased (see Figs. 5 and 16). This result occurred because the birds tended not to stay on the *long* side much time after the long duration had elapsed. Rather they started to move along the box and then pecked the key that they were facing at the moment of choice—hence, the proportion of *long* choices approached 0.5. Third and more qualitatively, we observed the acquisition of highly stereotypical behavioral patterns while the birds waited on each side. To illustrate, on the *short* side most birds engaged in vigorous pacing along the wall, with their breasts touching the wall; on the *long* side some birds oriented to one of the corners of the wall whereas others air pecked the key. The waiting patterns on the two sides were often different but they shared one feature, namely, the birds were always fac-

ing the corresponding key, the *short* key for patterns executed on the *short* side, and the *long* key for patterns executed on the *long* side. These orientations may have prevented many choice errors.

Finally, the results of Experiments 1 and 2 also show that during the first sessions in which choice performance was above chance, the means of the Departure times already were in the neighborhood of their final values, but the standard deviations remained substantially higher than their final values. In fact much of the effect of additional training seemed to consist in reducing the variability of the motion patterns during the trial. Hence, the superposition of the behavioral distributions seemed to improve with training (see Figs. 2–4, 7 and 9).

5.1.2. Correlation patterns

In Experiments 1 and 2, the correlation between Arrival and Departure times was moderately positive, whereas the correlation between Arrival and Residence times was weakly negative. This pattern of findings was reported by Gibbon and Church (1992) in the peak procedure: On some percentage of trials key pecks are reinforced when a fixed interval has elapsed since the signaled onset of the trial; on the remaining trials, the signal remains on for a substantially longer interval and responding is not reinforced. At the steady state, responding on nonfood trials shows three distinct states: pigeons peck at a low or zero rate at the beginning of the trial, at a higher rate around the time of food, and again at a low rate at the end of the trial. These three states define two moments on each trial, the start of the pecking state, akin to our Arrival time, and the end of the pecking state, akin to our Departure time. The authors report average correlations of 0.32 between Arrival and Departure times and -0.45 between Arrival and Residence times. The former value is within the range of correlations obtained in our Experiments 1 and 2, but the latter value is substantially more negative than what we have obtained.

The same correlation pattern was reported by Killeen and Fetterman (1993) using a three-key peak choice procedure in which reinforcers were available from pecking the right key at 8 s into the trial, the center key at 16 s into the trial, or the left key at 32 s into the trial. At the steady state the birds initiated the trial by pecking the right key, then switched to

the center key, and finally ended the trial pecking at the left key. The moment the birds switched from the right to the center key is analogous to our Arrival time and the moment they switched from the center to the left key is analogous to our Departure time. With three pigeons Killeen and Fetterman found correlations of 0.37, 0.49, and 0.64 between Arrival and Departure times and correlations of -0.14 , -0.11 , and -0.16 between Arrival and Residence times. Both sets of values are within the range of values we have obtained in Experiments 1 and 2.

Gibbon and Church (1992) and Killeen and Fetterman (1993) interpreted the pattern of correlations between Arrival, Departure, and Residence times in terms of Scalar Expectancy Theory and the Behavioral Theory of timing, respectively, and we refer the reader to the original articles for details. Here we will offer yet another interpretation of these correlations, an interpretation suggested by observations of the birds during our three experiments. Pigeons arrive at the *short* side at different moments since trial onset. In fact the variability of Arrival may be substantial during the early sessions of training. On short trials, when a bird arrives early to the *short* side it will wait longer for food than when it arrives late. That is, on the short trials the bird experiences directly, so to speak, a negative correlation between its Arrival and Residence times. But how does the bird wait? Typically it engages in what one might call a waiting pattern, a vigorous pacing along the wall of the *short* side. If the experienced negative correlation causes the waiting pattern to be executed *slightly* faster the later the bird arrives at the *short* side—where ‘slightly’ means that the increase in speed is small compared with the delay in Arrival—then (a) the correlation between Arrival and Residence times will be weakly negative because of the increase in the average speed of executing the waiting pattern, and (b) the correlation between Arrival and Stop will be moderately positive because the increase in speed is small and insufficient to offset the increase in Arrival. To put it differently, from the equality, $\text{Departure} = \text{Arrival} + \text{Residence}$, and the assumptions that an increment in Arrival (ΔA) leads to a decrement in Residence (ΔR), but $|\Delta A|$ remains much greater than $|\Delta R|$, we conclude that increasing Arrival will decrease Residence slightly but increase Departure moderately.

The empirical adequacy of this account remains to be tested.

To close a strongly empirical study, a conceptual remark may not be out of place. Philosopher Wittgenstein once suggested that when one is dealing with the intricacies of hypothetical internal processes it is always a good exercise to attempt to externalize them and proceed from there. In his words, “There is one way of avoiding at least partly the occult appearance of the processes of thinking, and it is, to replace in these processes any working of the imagination by acts of looking at real objects” (Wittgenstein, 1958, p. 4). The standard bisection task is considered a retrospective timing task and one is often tempted to explain the performance it engenders in pigeons and rats by invoking such internal processes as looking back at the sample, consulting memories of the signals, and the like. Perhaps then it would be worthwhile to try to externalize these intricacies—for example, by changing a (presumed) retrospective task into an ongoing timing task. This was precisely what the separation of the keys and the tracking of the animal’s motion during the trials attempted to achieve. We have also attempted to invoke the interactions of the animal with the contingencies of reinforcement (e.g. its experience of a negative correlation between Arrival time and delay to reinforcement during the short trials) to account for its steady state behavior. As much as possible, what is internal and hypothetical was replaced by what is external and at least potentially observable and measurable.

References

- Catania, A.C., 1970. Reinforcement schedules and the psychophysical judgments: a study of some temporal properties of behavior. In: Schoenfeld, W.N. (Ed.), *The Theory of Reinforcement Schedules*. Appleton-Century-Crofts, New York, pp. 1–42.
- Church, R.M., Deluty, M.Z., 1977. Bisection of temporal intervals. *J. Exp. Psychol.: Anim. Behav. Process.* 3, 216–228.
- Gallistel, C.R., 1990. *The Organization of Learning*. MIT, Cambridge.
- Gibbon, J., 1977. Scalar expectancy theory and Weber’s law in animal timing. *Psychol. Rev.* 84, 279–325.
- Gibbon, J., 1981. On the form and location of the psychometric bisection function for time. *J. Mathem. Psychol.* 24, 58–87.
- Gibbon, J., Church, R., 1992. Comparison of variance and covariance patterns in parallel and serial theories of timing. *J. Exp. Anal. Behav.* 57, 393–406.

- Killeen, P., Fetterman, G., 1993. The behavioral theory of timing: transition analyses. *J. Exp. Anal. Behav.* 59, 411–422.
- Killeen, P., Fetterman, G., Bizo, L.A., 1997. Time's causes. In: Bradshaw, C.M., Szabadi, E. (Eds.), *Time and Behaviour: Psychological and Neurobiological Analyses*. Elsevier Science Publishers, Amsterdam, pp. 79–131.
- Leak, T.M., Gibbon, J., 1995. Simultaneous timing of multiple intervals: implications of the scalar property. *J. Exp. Psychol.: Anim. Behav. Process.* 21, 3–19.
- Machado, A., 1997. Learning the temporal dynamics of behavior. *Psychol. Rev.* 104, 241–265.
- Machado, A., Keen, R., 1999. Learning to time (LET) or scalar expectancy theory (SET)? a critical test of two models of timing. *Psychol. Science* 10, 285–290.
- Platt, J.R., Davis, E.R., 1983. Bisection of temporal intervals by pigeons. *J. Exp. Psychol.: Anim. Behav. Process* 9, 160–170.
- Richelle, M., Lejeune, H., 1980. *Time in Animal Behavior*. Pergamon Press, Oxford, UK.
- Roberts, W., 1998. *Principles of Animal Cognition*. McGraw–Hill, New York.
- Wittgenstein, L., 1958. *The Blue and Brown Books*. Harper & Row, New York.