TIMING MULTIMODAL EVENTS IN PIGEONS

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The peak procedure was used in two experiments to study pigeons' ability to time multimodal events. In the first experiment, birds were trained to time a single event consisting of a 9-s tone or light followed by a 21-s fixed interval associated with a signal of light or tone (signal of the other modality). On occasional empty trials, different lengths of the first signal were followed by a long period of the second signal. Peak response times as a function of the duration of the first signal were linear and had a slope of close to one in all birds. This indicates that the birds were timing only the second signal. In a second experiment, two complex events were used in training. One consisted of a 9-s tone or light followed by a 21-s fixed interval associated with a light or tone. The other consisted of a 21-s tone or light followed by a 9-s fixed interval associated with a light or tone. Different durations of the first signal were again used on empty trials. Peak response times as a function of the duration of the first signal were again linear in all birds. The slope of the function was less than one but greater than zero for 3 birds. This indicates that these birds were partly timing the entire complex event of 30-s duration and partly timing only the second signal of the event. A model is proposed in which the bird takes as a criterion for timing a weighted average of different target criteria. Comparisons with the performance of rats are made.

Key words: timing, peak procedure, internal clock, multimodal, key peck, pigeon

Recent experimental studies of timing in rats and pigeons have revealed some differences between the two species in timing strategies. One difference is found when animals are presented with multimodal stimuli in the peak procedure. In the peak procedure, an animal is trained on a fixed-interval (FI) schedule to some signal, usually a light or a tone. When a scallop has developed, the subject is occasionally tested on empty trials. Here, the signal runs on for far longer than its usual duration, and responding on the trial is unrewarded. In this case, both rats (S. Roberts, 1981, 1982) and pigeons (W. Roberts, Cheng, & Cohen, 1989) show a roughly normal distribution of response rate as a function of time, with the peak at around the time of the FI. Rats and pigeons can also be trained to discriminate between light and tone signals associated with different durations. They show peaks at times appropriate to each stimulus on empty trials (S. Roberts, 1981, 1982; W. Roberts et al., 1989).

Species differences are found, however, when a signal is changed in the middle of an empty

trial. Suppose for illustration purposes that rats and pigeons were trained to time a 15-s tone and a 30-s light. On an empty trial, the tone was presented for 6 s and followed by an extended period of light. In that case, rats peak in response rate at around 30 s from the beginning of the tone signal (S. Roberts, 1981), whereas pigeons peak at around 36 s from the beginning of the tone signal (W. Roberts et al., 1989). In general, the time of peak response rate for the pigeons is delayed from its usual time (about 30 s) by the duration of the tone.

One interpretation of this observation is that the two species use their internal clocks differently under these circumstances. The rats are said to keep the clock running as the signal changes. When the signal changes, they time the new signal with the amount already accumulated on the clock left intact (S. Roberts, 1981). In our example above, when the signal changes, they attempt to time a 30-s period with 6 s of time already having elapsed on the clock. They thus show a peak rate of response 24 s later, or 30 s from the beginning of the tone. Rats are in effect timing a multimodal event consisting of a light following a tone. Pigeons are said to reset their internal clocks upon a signal change. As the clock goes back to zero at the signal change, their time of peak response rate comes at 30 s after the signal change. The birds are thus delayed in the time

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of peak response rate by about the duration of the preceding signal (W. Roberts et al., 1989). Thus, the rat's natural propensity is to keep the clock running through signal changes, whereas the pigeon's natural propensity is to reset the clock at a signal change.

We have cast the difference as one of propensity or choice of timing strategy. It might be wondered whether pigeons can learn to time a multimodal signal if given appropriate training. No evidence is yet available to show that pigeons can in fact time a multimodal event or keep the clock running through a change in the nature of the signal. In the experiments reported here, we have progressively introduced conditions that required timing a multimodal event. In the first experiment, the birds were trained to time one multimodal event consisting of a light of a fixed duration followed by a tone (or vice versa). Here, the duration of the second signal predicted the arrival of the food perfectly. We expected the pigeons to time the duration of the second signal and ignore the light-tone complex event. In the second experiment, two complex events of the same total duration were used in training. Both consisted of a light followed by a tone (or vice versa). However, the component durations of the tone and light were different for the two events. Thus, the duration of the second signal did not predict the arrival of food accurately, whereas the duration of the complex event did. Under these conditions, evidence of timing a complex event may appear in the pigeon.

EXPERIMENT 1

In Experiment 1, the birds were trained to time a single complex event. This consisted of a 9-s signal (tone or light) followed by a 21-s signal (light or tone). The subjects were tested with occasional empty trials in which a first signal of varying duration was followed by a second signal making up a total time of 90 s. No rewards were dispensed on such trials. The pecking rates on these trials as a function of time constituted the data analyzed. The first signal on the empty trials lasted 3 s, 9 s, or 15 s.

The variation in the time of the peak pecking rate allows us to determine how the bird is timing the complex event. At least two possibilities arise. The birds may time only the

second signal, that which immediately precedes the food delivery. In that case, the time of peak pecking rate ought to be different for different durations of the first signal on the empty trials. The time of peak pecking rate as a function of the duration of the first signal ought to have a slope of one. A second possibility is that the birds time a 30-s complex event whose nature changes in the middle of the event. In that case, the time of peak pecking rate ought to be around 30 s no matter what the duration of the first signal. The time of peak pecking rate as a function of the duration of the first signal ought to have a slope of zero. An intermediate slope between zero and one would indicate some compromise between the two strategies.

METHOD

Subjects

Five White King pigeons (*Columba livia*) served as subjects. They had all served in other experiments in operant chambers, and 2 had served in experiments on foraging and spatial memory as well. None had participated in timing experiments before. The birds were maintained at approximately 80% of their free-feeding body weights throughout experimentation and had constant access to water and health grit.

Apparatus

An operant chamber was used that measured 31 cm by 35.5 cm (floor dimensions) by 35.3 cm (wall height). The front wall contained a row of three pecking keys level with the pigeon's head, spaced 8 cm apart center to center. Only the right key was used. A projector mounted behind the key illuminated it with white light. The key was always lit throughout experimentation. An electromechanical food hopper provided mixed grain through a 6-cm by 6-cm opening centered on the front wall below the pecking keys. A 6-W lightbulb covered with a red lens located on the ceiling provided the light stimulus used in the experiments. A speaker in the lower left corner of the key panel provided tone stimuli.

All trial events and data recording were controlled by a Commodore 64® computer and a locally constructed interface. A 79-dB tone of 1,325 Hz was programmed through the com-

puter and played through the speaker in the operant chamber.

Procedure

Pigeons were initially trained to peck the illuminated right side key for grain reinforcement. The experiment began when all birds were readily pecking at the key. Three birds were assigned to the tone-light group and 2 to the light-tone group. Each animal was tested for one session each day that consisted of 36 training trials and 12 empty trials. The order of the trials was chosen randomly, subject to the constraints that (a) in a block of eight trials, two were empty trials, and (b) at least two training trials preceded each empty trial. The same order was used for all birds throughout the experiment.

A training trial began with only the keylight on. A 9-s signal then occurred. This was a tone for the tone-light group and a light for the light-tone group. After 9 s, the tone or light ended and a second signal replaced it immediately. This was a light for the tone-light group and a tone for the light-tone group. The first key peck after 21 s of the second signal was reinforced with 2-s access to the food hopper. An empty trial also began with only the keylight on. The 9-s signal was followed by a second signal of 81-s duration. No reinforcement was dispensed. Intertrial time varied randomly between 10 s and 40 s. During this time, only the keylight was on.

The birds were studied in the same order each day, starting at about 7:30 a.m., so that each animal was studied at about the same time each day. They were trained for 20 days, at which point behavior appeared to have become stable. After that, three different kinds of empty trials were used. Each kind was composed of two different signals of 90 s in total duration, but they differed in the duration of the first signal, which was either 3 s, 9 s, or 15 s long. These conditions are called the 3-87, 9-81, and 15-75 conditions. On all empty trials, the tone-light group continued to receive tone as the first signal, and the light-tone group continued to receive light as the first signal. On each day, every empty trial was of one kind for each bird. Over a 3-day block, all three kinds of empty trials were used. The birds were studied for 21 sessions, and data from the last 15 sessions were analyzed.

Data Analysis

The data from empty trials were summarized by plotting the mean pecking rates in successive 3-s bins throughout the 90-s duration of the signal. For each bird in each condition, peak times and peak rates were calculated on the pooled distribution of pecking rates according to a procedure used by S. Roberts (1981). For peak time, an initial median time was calculated. A second median was calculated based on a distribution equidistant on each end from the initial median. This procedure was continued until the medians on iterations n and $n - 1$ did not differ by more than 0.05 s. The median calculated on the n th iteration was the peak time. It should be pointed out that this formal procedure does not always yield a peak time in the modal bin. Rather, the calculation yields what intuitively corresponds to the middle of the highest region of the distribution. It is preferable to the mode because the modal bin might have the highest number of responses due in part to unsystematic error. It is also preferable to the mean and median in that these latter measures of central tendency do not yield the middle of the highest region for skewed distributions. Peak rate was the rate of responding at the peak time and was calculated by linear interpolation between the two bins on either side of the peak time. It does not necessarily correspond to the response rate in the modal bin.

RESULTS

In the last 5 days of training (Sessions 16-20), the birds' pooled data revealed a peak time of 31.3 s. The distribution was single peaked and resembled that found in the test phase for the 9-81 condition.

Peak times in the test phase were calculated separately for each bird. The average across birds is shown in Figure 1. (Pooling the data from all birds first in each condition and then calculating peak times gives similar results.) A best fit straight line for the three points was calculated using a least squares criterion. The resulting slope of the function was close to one. The small standard error of estimate indicates that a straight line was indeed an excellent fit of the data. Individual patterns did not differ significantly from the mean. Peak times and peak rates are presented for each pigeon in

Fig. 1. Peak time (averaged across birds) as a function of the duration of the first signal in Experiment 1 (open circles) and in Experiment 2 (filled circles). The equations show best fitting straight lines according to a least squares criterion. The standard error of estimate was 0.34 for Experiment 1 and 0.07 for Experiment 2.

Table 1. Best fit straight lines according to a least squares criterion are presented in Table 2. It can be seen that all birds show straight lines with slopes close to one. The five best fit slopes do not differ significantly from 1.0 as a group, according to a *t* test. Except for Bird 8, the intercepts of the functions are around 21 s, indicating that the birds peaked in their response rates about 21 s after the signal change. Bird 8, for reasons unknown, peaked substantially later than the FI period of 21 s.

The distribution of pecks, pooled over birds, is shown in Figure 2. Each individual bird also shows single-peaked functions. Figure 2 and Table 1 also show that the peak rates of pecking were similar in all conditions. Table 3 shows that the widths of the distributions were similar in all conditions for all birds. Width was calculated by taking the difference in time between the two points nearest to the peak time in the function at which the response rate was half of the peak rate. Response rates were linearly interpolated between bins. A within-subjects analysis of variance of the widths revealed no significant differences across conditions (*F* = 3.21).

DISCUSSION

The time of the peak pecking rate of the birds was displaced systematically according

Table 1

Peak times in seconds and peak rates in pecks per minute (in parentheses) for individual birds in Experiment 1.

Bird	Condition		
	3-87	9-81	15-75
Tone-light group			
1	23.1 (68.5)	29.2 (63.6)	36.1 (69.4)
8	30.3 (64.0)	37.3 (65.5)	41.2 (51.4)
6	26.3 (74.4)	32.6 (82.6)	40.2 (69.8)
Light-tone group			
2	23.2 (58.1)	30.4 (84.9)	35.9 (91.6)
10	25.2 (56.5)	32.3 (58.7)	40.5 (49.0)

to the duration of the first signal in a complex event. The amount of displacement corresponded to the difference between the duration of the first signal during training and testing. If the first signal on a test was 6 s shorter than usual (the 3-87 condition), the birds peaked about 6 s earlier. If the first signal was 6 s longer than usual (the 15-75 condition), the birds peaked about 6 s later than usual. It thus appears that the birds were timing only the duration of the second signal. They showed no evidence of timing the complex event at all. Because half the birds encountered events in the order light-tone and half encountered events in the order of tone-light, we can conclude that the event closer to the reinforcer is predominant regardless of the nature of the signals.

EXPERIMENT 2

This experiment again tested the possibility that pigeons might time a complex event con-

Table 2

Best fitting straight lines by the least squares criterion of peak times as a function of the duration of the first signal for individual birds in Experiment 1.

Bird	Function	Standard error of estimate
Tone-light group		
1	$Y = 1.077X + 19.771$	0.21
8	$Y = 0.913X + 28.034$	0.72
6	$Y = 1.160X + 22.606$	0.32
Light-tone group		
2	$Y = 1.060X + 20.274$	0.42
10	$Y = 1.280X + 21.146$	0.23

Fig. 2. Pecking rate (averaged across birds) as a function of time in the three conditions of Experiment 1.

sisting of a light and a tone in sequence. Conditions encouraging the timing of a complex event were introduced by training birds with two complex events. One event consisted of 9 s of a first signal followed by the second signal of a different modality, as before. The other complex event consisted of 21 s of the first signal followed by the second signal of a different modality. In both cases, the reward was delivered for the first peck after 30 s from the start of the complex event. Thus, the duration of the second signal before the delivery of food now varied, but the duration of the complex event before the availability of food remained constant at 30 s.

Birds were again tested with empty trials in which the duration of the first signal varied from 3 s to 27 s. Again, if they timed only the second event, using some averaged reference memory of the different durations of the second event before food delivery, the peak times should vary systematically as a function of the duration of the first signal. Peak time as a function of the duration of the first signal should be linear with a slope of one. If they timed only the 30-s duration of the complex event, peak times as a function of the duration of the first signal should have a slope of zero. An intermediate slope would indicate a compromise between the two strategies.

Table 3

Widths of pecking distributions in time (in seconds), defined as the time interval between the two times at which the pecking rate is 50% of the peak pecking rate, in Experiment 1.

Bird	Condition		
	3-87	9-81	15-75
Tone-light group			
1	17.1	17.4	17.0
8	18.6	15.9	19.3
6	14.4	16.2	16.6
Light-tone group			
2	20.0	21.4	22.7
10	24.9	25.8	27.2

METHOD

Pretraining. The same subjects continued to participate. They were first trained for two sessions with the new complex signal, which consisted of 21 s of the first signal followed by a second signal of a different modality. Food was delivered for the first peck after 9 s of the second signal. Birds in the tone-light group continued to have tone as the first signal, and birds in the light-tone group continued to have light as the first signal. The animals were then trained for 3 days with both complex signals. A random half of the trials consisted of a 9-s first signal followed by the second signal; the other half had a 21-s first signal followed by a second signal. No empty trials were conducted for these 5 days.

Phase 1. The animals continued for 22 sessions on the training regime with two complex events, but empty trials, 12 per session, were included. On half of the days, the empty trials consisted of a 9-s first signal followed by an 81-s second signal. On the other half, the empty trials consisted of a 21-s first signal followed by a 69-s second signal. The last four sessions (two of each condition of testing) were analyzed.

Phase 2. The results showed different peak times for the two test conditions. We wanted to ensure that the birds had learned something of the new training event, that is, the one with the 21-s first signal. For the next 5 days, then, the birds were trained only with that event, with 12 empty trials included in each session. On these empty trials, the first signal was 21 s in duration, the second signal 69 s.

Phase 3. The results from Phase 2 indicated

that the animals as a group had learned to adjust their behavior with the new training event. They were then tested for five more sessions with both training events to ensure that the behavior obtained in Phase 1 represented steady-state behavior. Once again, half of the training trials had a 9-s first signal, and half had a 21-s first signal. Empty trials were included. On odd days, the first signal on empty trials lasted 9 s, and, on even days, it lasted 21 s. Again, the total duration of empty trials was 90 s.

Phase 4. Having ensured that the behavior under the new training conditions was asymptotic, testing with the crucial conditions then began. The birds were tested for 30 days with five different empty-trial conditions. Each was a complex event lasting 90 s, but the duration of the first signal varied. It was either 3 s, 9 s, 15 s, 21 s, or 27 s, and these conditions are called the 3-87, 9-81, 15-75, 21-69, and 27-63 conditions, respectively. In each session, only one condition was used. The conditions rotated in each block of 5 days.

In each block of eight trials, two were empty. At least two training trials preceded every test trial. Training trials beginning with either a 9-s or 21-s signal preceded an empty trial equally often. One order of training and test trials was used for all birds throughout experimentation. Data from the last 25 days were analyzed.

RESULTS

In Phase 1, after 22 days of training with two types of complex events, the birds' peak times differed according to the duration of the first signal on empty trials. The response-rate distributions in the last four sessions were pooled across birds. On the pooled distributions, the peak time for the 9-81 empty trials was 28.0 s (peak rate 75.7 pecks/min) and the peak time for the 21-69 empty trials was 36.9 s (peak rate 75.4 pecks/min).

In Phase 2, when the birds were trained solely with a single complex event whose first signal was 21 s long, they on the whole adjusted their peak time. On Sessions 4 and 5, the peak time for the pooled distribution of 21-69 empty trials was 32.4 s (peak rate 77.5 pecks/min).

In Phase 3, after being trained with two types of complex events again (half having a 9-s first signal, half a 21-s first signal), the

peak times on the whole resembled those found in the first phase of this experiment. For the pooled distribution of the 9-81 empty trials, peak time was 27.4 s (peak rate 67.5 pecks/min); for the 21-69 empty trials, it was 36.5 s (peak rate 68.7 pecks/min). It appears that the behavior pattern obtained after the training in Phase 1 was asymptotic.

In the crucial last phase of the experiment, in which five different durations of first signals were used on empty trials, the peak times for each bird again varied as a function of the duration of the first signal. The patterns differed between birds, and individual distributions are shown in Figure 3. Three birds (1, 2, and 10) showed single-peaked functions in each condition. Bird 8 showed clear double-peaked functions for the 15-75, 21-69, and 27-63 conditions and single-peaked functions for the other two conditions (3-87 and 9-81). The secondary peaks in each case occurred just before the signal changed from tone to light. Bird 6 showed hints of double-peakedness in each distribution.

Peak times and peak rates were calculated according to the usual formula for each bird, and they are presented in Table 4. Mean peak time as a function of the duration of the first signal is shown in Figure 1. The points are obtained from calculating peak times for individual birds and then averaging across birds. (Pooling the data from all birds first and then calculating peak times for the resulting distributions yields similar results.) The resulting function was linear, with the slope of the best fitting line being 0.76. Best fit functions were also calculated for individual birds (Table 5). Although straight-line fits are reasonable or excellent in all birds, it can be seen that the slopes of the function differed across birds. Two birds did not deviate substantially from one. The birds as a group, however, had an average slope less than one ($t = 8.14$, $p < .01$, two-tailed).

In comparison to Experiment 1, Birds 2 and 10 had larger intercepts, Birds 6 and 8 had smaller intercepts, and Bird 1 had about the same intercept as before. Widths of distributions are presented in Table 6. Again, width was defined as the difference in time between the two points nearest the peak time at which the response rates were at 50% of the peak rate. Except for those of Bird 8, widths of distributions were again similar in all con-

ditions. Bird 8 had wider distributions in the 15-75, 21-69, and 27-63 conditions because doubled-peaked functions were found in these conditions. The birds as a group, however, showed similar widths in all conditions. A within-subjects analysis of variance on widths revealed no significant differences across conditions ($F < 1$).

DISCUSSION

Different patterns of results were obtained for different pigeons. For Birds 2, 8, and 10, the peak time was a linear function of the duration of the first signal with a slope less than one. Bird 8, however, showed secondary peaks in three of its distributions just before the signal changed from tone to light, whereas Birds 2 and 10 produced single-peaked functions in all distributions. Birds 1 and 6 produced peak times that were a linear function of the duration of the first signal with a slope of about one. Thus, they seemed to have timed only the second signal in the complex event. But what accounts for the performance of Birds 2, 8, and 10?

For these 3 birds, peak times were displaced as a function of the duration of the first signal of the complex event. But a 6-s difference in the duration of the first signal here led to a shift of peak time of only 4 s, not 6 s, as in Experiment 1. Our interpretation is that the pigeons use a single internal clock for timing but have two reference memory durations that are averaged to obtain a single criterion time in each empty trial condition. One reference memory duration is obtained from timing only the second signal. It has some fixed value from the start of the second signal, with different birds having different values. A second reference memory value is obtained from timing the entire 30-s complex event and has a value of about 30 s from the start of the first signal.

To illustrate the model more precisely, two idealized concrete cases are illustrated in Figure 4. Suppose that the model bird had been trained with complex events consisting of a tone signal followed by a light signal. The two columns illustrate how the bird behaves in a situation consisting of a 3-s tone followed by a long period of light or a 27-s tone followed by a long period of light. The elements of the timing system resemble in essential respects what has been proposed for the rat (Gibbon & Church, 1984; S. Roberts, 1981, 1982). We

Fig. 3. Pecking rate for individual birds as a function of time in Phase 4 of Experiment 2. Only the range of the distribution where the response rate was high is shown. The range includes the first bin on either side of the bin with the most responses whose response rate is below 50% of the maximal bin. The numbers on the graphs refer to the duration of the first signal.

Table 4

Peak times in seconds and peak rates in pecks per minute (in parentheses) for individual birds in Phase 4 of Experiment 2.

Bird	Condition				
	3-87	9-81	15-75	21-69	27-63
Tone-light group					
1	24.8 (39.5)	29.6 (37.1)	36.8 (39.4)	42.0 (49.3)	47.6 (53.5)
8	21.2 (51.2)	26.6 (53.0)	27.3 (49.9)	31.7 (47.9)	35.8 (50.0)
6	22.9 (43.2)	27.3 (43.5)	34.1 (39.6)	41.0 (45.5)	45.8 (45.5)
Light-tone group					
2	24.1 (104.7)	27.6 (113.7)	31.8 (119.4)	36.3 (119.0)	40.6 (111.6)
10	26.6 (85.5)	30.5 (96.0)	30.7 (100.9)	35.0 (103.9)	41.3 (105.0)

suppose that the timing device, the clock itself, consists of an accumulator and a gate. When the gate is open, regular pulses fill the accumulator. The level in the accumulator (the number of pulses) represents the time elapsed since the clock began to time. In addition to the clock, the system has a memory, which governs how the animal behaves as a function of the reading on the clock. The memory starts, stops, and resets the clock. It also sets a criterion, the level of the clock at which maximum response rate is to be found. Response rate increases as the criterion is neared and decreases as the criterion is passed. We suppose that the system has but one clock.

When the tone starts (0 s), two things happen: The gate of the clock is opened and the bird begins to time. Also, a criterion is set at approximately 30 s, the remembered duration of the entire complex event. This is indicated by the solid arrow in Figure 4. When the tone changes to light, at 3 s for one event and at 27

s for the other, an adjustment to the criterion is made. The light dictates a second criterion time. We have taken an arbitrary criterion value of 15 s from the onset of the light. These are shown by the dotted arrows. When tone changes to light at 3 s, this criterion associated with the second signal is at 18 s. When tone changes to light at 27 s, this second criterion is at 42 s. Thus, in both cases, two forces drive the bird to different criterion levels. In both cases, the bird takes a weighted average of the two values. In the example, the weight is about .75 for the criterion associated with the second signal and .25 for the criterion associated with the entire complex event. In our example, for an event of 3-s tone followed by light, the criterion is set at about 21 s, and, for an event of 27-s tone followed by light, the criterion is set at about 39 s. The animal then follows this new criterion. The peak times thus generated, when plotted against the duration of the first

Table 5

Best fitting straight lines by the least squares criterion of peak times as a function of the duration of the first signal for individual birds in Phase 4 of Experiment 2.

Bird	Function	Standard error of estimate
Tone-light group		
1	$Y = 0.962X + 21.726$	0.45
8	$Y = 0.573X + 19.942$	0.93
6	$Y = 0.989X + 19.391$	0.64
Light-tone group		
2	$Y = 0.689X + 21.749$	0.25
10	$Y = 0.563X + 24.371$	1.42

Table 6

Widths of pecking distributions in time (in seconds), defined as the time interval between the two times at which the pecking rate is 50% of the peak pecking rate, in Phase 4 of Experiment 2.

Bird	Condition				
	3-87	9-81	15-75	21-69	27-63
Tone-light group					
1	21.2	22.7	23.2	23.1	21.9
8	25.9	29.9	40.1	45.3	45.1
6	27.5	24.4	26.1	23.8	24.7
Light-tone group					
2	23.9	26.8	27.2	26.1	24.7
10	25.2	20.5	19.4	18.4	18.7

3s TONE, 87s LIGHT

27s TONE, 63s LIGHT

Os

3s

27s

Fig. 4. A model of the timing system. A model bird had been trained with events consisting of a 9-s tone followed by a 21-s FI on a light or a 21-s tone followed by a 9-s FI on a light. The timing system consists of a clock that keeps time and a memory that governs response as a function of the reading on the clock. How the model bird behaves in

signal, will produce a straight line with the slope corresponding to the weight given to timing the second signal. Thus, as long as the bird is not timing only the second signal, the slope will be less than one. The weight given to timing the second signal varies from bird to bird, as Table 5 shows.

Only one addition to the system needs to be added in the cases of Birds 2 and 10. In Figure 3, their response rate in the presence of the first signal never rises substantially. According to the model, the response rate ought to follow the initial criterion of 30 s until the signal change. In the case of a long first signal (e.g., 27 s), the response rate ought to rise substantially before falling again in the face of criterion adjustment at the signal change. Such a pattern is found with Bird 8, who exhibited secondary peaks just before the signal change when the duration of the first signal was 15 s or longer. Decreases in response rates just after a signal change have also been found in pigeons trained in paradigms different from those used here (W. Roberts et al., 1989, Figures 5, 6, 8, and 9). To explain why response rate never rose in the presence of the first signal for Birds 2 and 10, we suppose that the first signal acted as an inhibitory signal. This is reasonable, because the presence of the first signal was never associated with the availability of food. We suppose that the birds learned to suppress responding in the presence of the first signal regardless of the dictates of the timing system. Other explanations can also be proposed, but we find the inhibition explanation most natural and plausible.

For Birds 1 and 6, the slope of the function of peak time against duration of first signal was one. Thus, each 6-s increase in first-signal duration led to a delay in peak time of about 6 s. This indicates that they were timing only the second signal. In the case of Bird 6, hints of double-peakedness were found in every distribution. A formal attempt was made to calculate both peaks of the distribution separately. This was done by dividing the distribution into two halves and calculating the

peak times of each half using the standard formula. The distribution was divided at the locally minimal bin between the two peaks. (The locally minimal bin itself was included in the calculation of both peaks.) The later peak times thus calculated virtually replicated those shown in Table 4, where the calculation was done over the entire distribution. Most likely, this calculation process was not successful at identifying the second peak time in the distributions.

The earlier peak times were as follows: 14.5 s for the 3-87 condition, 20.0 s for the 9-81 condition, 27.7 s for the 15-75 condition, 34.1 s for the 21-69 condition, and 37.2 s for the 27-63 condition. The best fit straight line is $Y = 0.993X + 11.822$, with a standard error of estimate of 1.07. Thus, this peak comes about 11.8 s after the signal switch in each condition. When the bird was timing a 21-s FI (of the second signal) in Experiment 1, its peak time was at about 24.0 s after the start of the second signal, about 3 s later than the FI period. The 11.8-s intercept here corresponds to a time 2.8 s later than a 9-s period, the FI associated with the second signal for one of the types of training event. This suggests that, in the first of the double peaks, Bird 6 was timing a 9-s duration from the point at which the signal switched. The later peak, as estimated by the peak times given in Table 4, comes about 19.4 s after the signal switch (Table 5). It is thus 1.6 s earlier than 21 s, the FI associated with the second signal in the other type of training event. Given that the bird usually peaks some 3 s after the FI duration, the peak times are too early. The calculation procedure, however, might well err on the early side in this case because the earlier peaks would distort the calculation in the earlier direction. It seems plausible, then, that this bird showed two peak times in each of its distribution, each peak timing the FI duration for the second signal in each of the types of training event. In any case, it seems reasonable to argue that this bird showed double-peaked distributions. This might mean that it was timing with two clocks, set at different criteria,

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the presence of a 3-s tone followed by a long period of light and a 27-s tone followed by a long period of light is illustrated. A tone in either case dictates a criterion setting of 30 s, and the light signal dictates a criterion time that is 15 s from its onset. The bird takes a weighted average of the target criterion levels to set a criterion. For further explanation, see text.

or timing with a single clock using two criterion markers. We prefer the latter interpretation. The model for Birds 2, 8, and 10 postulates the averaging of different criteria. The explanation of their results requires that only a single clock be postulated. Two criteria cannot be averaged to yield one criterion if they are for different clocks. It seems more parsimonious to suppose that all pigeons possess a single internal clock in their timing system.

One other plausible alternative, that the birds were solving the problem by conditional discrimination, can be ruled out by the data. In this model, the bird times only the second signal but uses the duration of the first signal as a conditional signal for setting a criterion to time the second signal. If the first signal is judged to be long (21 s), then the criterion for timing the second signal is set at 9 s. If the first signal is judged to be short (9 s), then the criterion for timing the second signal is set at 21 s. It is not clear that the model would predict a linear function of peak times against duration of first signal. At least we can find no principled reason why they should be linear under this model. The most telling refutation, however, comes in the 15-75 condition. Here, the duration of the first signal was between the two first-signal durations (9 s and 21 s) found during training. This ought to produce double-peaked distributions with a peak time at each of the peak times found in the 9-81 and 21-69 conditions. For no bird was this the case. It might be supposed that a double-peaked function was in fact found in this condition, but that the two peaks have merged together into a single peak. In this case, we should at least expect the distribution for the 15-75 condition to be wider. Table 6 shows that this was not the case.

GENERAL DISCUSSION

In these two experiments, we examined whether pigeons can be induced to time a complex event consisting of signals of two different modalities. The answer is: yes, partially. But in addition to answering the question we set at the beginning, an unexpected averaging process was discovered. The birds in Experiment 1 timed only the second signal of a complex event. But in Experiment 2, when they were exposed to two different complex events in

training, 3 of 5 birds showed evidence of timing a complex event that changed modality in its course. Pigeons are thus capable of timing multimodal events. Evidence also shows that all the birds timed the duration of the second signal, even though that signal varied in duration between 9 s and 21 s in training. The two timing processes were averaged in 3 of the birds, and we have argued that the averaging takes place in adjusting the criterion for the timing episode. Thus, the birds were in part timing the entire complex event.

The averaging model resembles in essential respects a timing model favored by S. Roberts (1982) for rats. Based on different paradigms, Roberts concluded that rats timed different signals with a single clock and a single memory. The clock is the system that times durations. The clock is taken to be a time-up device. This means that it starts timing from zero, and pulses accumulate on the clock as time passes. A time-up device works like a stop watch. This is in contrast to a time-down timing device, which starts with some fixed accumulation and runs down to zero. A time-down device works like a minute-minder. The memory is the process that reads the level of the clock and generates responses accordingly. Signals of different types (e.g., light vs. tone) are distinguished by the clock, even though both are timed by the same clock. Furthermore, the signals to be timed can directly affect the memory process by, for example, changing criterion levels.

The model for pigeon timing shown in Figure 4 concurs with all but one of these characteristics. We have argued that a single clock does the timing, and a single memory governs response output as a function of the clock. We have assumed the clock to be a time-up device because it is simpler to adjust criterion levels on a time-up device than on a time-down device. Furthermore, the memory is sensitive to the nature of the signal. A change in the modality of the signal affects the memory by readjusting the criterion position. What is not clear is whether the clock distinguishes different types of signals. Certainly peak times change in a sensitive fashion according to the particular mix of tone and light in an event. But we have posited a system in which the memory is sensitive to the nature of the signal. Because adjustments in the memory, specifically changing the level of the criterion, account for the

pattern of results, the clock need not distinguish what it is timing.

A New Look at Resetting

Previous research with pigeons has shown evidence of resetting (W. Roberts et al., 1989). In one experiment (Experiment 4), pigeons were trained to time a 15-s tone duration or a 30-s light duration. On some tests, a signal in one modality was started and then switched to a signal in the other modality. Peak times on such tests were delayed by the duration of the first signal. Thus, a 6-s tone followed by light resulted in a peak time around 36 s. It was as though the clock reset when the signal changed its nature.

Instantaneous resetting, however, has recently been questioned. Wilkie (1988) has found that pigeons show proactive interference in a choice paradigm. Pigeons were trained to make one response for a 2-s signal and another response for a 10-s signal. It was found that the length of the signal on the previous trial, with an intertrial interval of 2 s, affected how the birds performed on a 6-s signal. They chose long more often when the preceding trial was a 10-s duration. The clock, then, seems not to have been completely reset in 2 s. Our present model has a way of reconciling this delay in resetting with the instantaneous resetting posited by W. Roberts et al. (1989).

The present timing model also posits a resetting process, but the resetting does not consist of emptying the contents of the clock. Instead, it keeps the contents of the clock, but readjusts the criterion level. In the case of the data of W. Roberts et al. (1989), the two notions are indistinguishable. Whether the criterion is readjusted from 30 s to 36 s while the clock reads 6 s, or whether the clock is reset to 0 s and the criterion to 30 s when the signal changes modality from tone to light, the peak time would be about 36 s in both cases. In the present study, however, resetting of the clock does not account for the data well. If the clock were reset at the point of signal change, one would have to posit different degrees of resetting as a function of the duration of the first signal, at least for the 3 birds whose slope of the function of peak time against the duration of the first signal was less than one. It seems to us more elegant to suppose that the criterion is readjusted. Then, a weighted average of the

two target criterion levels would naturally produce a straight-line function with slope between zero and one. Add to these arguments Wilkie's (1988) evidence for incomplete clock resetting in 2 s, and the argument for the resetting of the criterion rather than the clock looks convincing.

This way of looking at resetting gives a reformulation of intermodal switch experiments that have been performed with rats (S. Roberts, 1981) and pigeons (W. Roberts et al., 1989, Experiment 4). For illustration, suppose that the animals had been trained to time 15 s under a tone and 30 s under a light. Now on a test, a 6-s tone is followed by light. The animals perform differently in these experiments. Rats keep the clock running through a signal change, peaking at around 30 s, whereas pigeons appear to reset, peaking at around 36 s. Under the new formulation, both species keep the clock running through the signal change. Only the criterion is adjusted differently in the two species. Rats choose a level appropriate for a complex event: The tone followed by the light should add up to 30 s. The pigeons choose a level appropriate for the second signal: 30 s since its start. We can account for the species difference here by a difference in the relative weight accorded to timing the complex event versus timing the second signal. Rats give more weight to the complex event; pigeons give more weight to the signal closest to food delivery. A strategic variation may be recast as a parametric variation.

Note that, although the evidence suggests that pigeons timed the duration of a complex event, they still placed most emphasis on timing the second signal. The slopes of the functions of peak time against duration of first signal for individual birds in Experiment 2 indicate that 2 birds timed only the second signal, whereas 3 birds had weights for timing the second signal ranging from .56 to .69. And in the first experiment, in which the birds encountered only one type of complex event, they timed the second signal exclusively. Even in Experiment 2, however, only two types of training events were used. It is possible that, when the birds are trained with even more types of complex events whose total duration is constant, they will weight the timing of the complex event more. In any case, that 3 of the birds weighted the timing of the second signal

less in Experiment 2 than in Experiment 1 indicates that the weighting parameter is flexible.

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