

Timing behaviour of black-capped chickadees (*Parus atricapillus*)

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Abstract

In Experiment 1 the behaviour of black-capped chickadees timing intervals of 12.5 or 37.5 s was studied using the peak procedure. Average rate of responding peaked near the trained FI on test trials, while the spread of the response distribution was larger for the longer FI. On individual trials, chickadees showed a break-run-break pattern of abrupt changes in rate of responding. These results, plus the pattern of means, standard deviations, and correlations found in start times, stop times, and durations of runs, were similar to those found in pigeons and rats. This suggests that birds and rodents use similar timing mechanisms. In Experiment 2, chickadees were tested with an interrupted FI signal. On such ‘gap’ trials, the chickadees, like pigeons but unlike rats tested under similar parameters, ignored the signal time elapsed prior to the FI interruption and reset the interval clock. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Timing behaviour; Black-capped chickadees; *Parus atricapillus*

1. Introduction

The timing behaviour of pigeons and rats has been the focus of investigation for many years. A number of properties of the timing mechanisms used during fixed interval (FI) responding, common to both pigeons and rats, have been identified. Typically, pigeons and rats are trained to respond on an FI schedule until stimulus control is established. At this point ‘empty trials’ are interspersed with normal FI trials. On an empty

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trial the signal continues after the trained interval, and no reinforcement is given. Tested using this 'peak procedure' (Catania, 1970), pigeons, rats, and humans produce nearly symmetrical distributions of response rates, with peaks of responding near the trained FI (e.g. Roberts, 1981; Rakitin et al., 1998; Cheng and Roberts, 1991) and demonstrate a linear increase in standard deviation as the FI increases, in accord with Weber's law (Gibbon and Church, 1984; Cheng and Roberts, 1991). These properties are most pronounced after extensive training (Kirkpatrick-Steger et al., 1996). They also manifest a break-run-break pattern of responding on individual trials; subjects switch abruptly from a low rate of responding to a burst of responding, which then terminates abruptly (Gibbon and Church, 1990; Cheng and Westwood, 1993; Church et al., 1994).

Three different theories have been proposed to account for behaviour on the peak procedure, and timing in general. Scalar Expectancy Theory (SET) (Gibbon and Church, 1984) has three components: (1) an interval clock that measures elapsed time; (2) a memory that holds times of reward and thresholds; and (3) a decision system that uses information from the other components to decide whether to respond at a high rate. The second model was developed by Church and Broadbent (1990) and is similar to SET. Their connectionist model contains the same components as SET, except that a number of oscillators take the place of the single clock in SET. In the Behavioral Theory of Timing (BeT; Killeen and Fetterman, 1988, 1993), the organism passes into various states, perhaps associated with its own behaviour, as time passes. States that become associated with reinforcement tend to generate high rates of responding. There is no decision process. All three models can account for the characteristics of the summed distributions on the peak procedure (i.e. symmetrical distributions, etc.), but only SET can account quantitatively for the patterns found on individual trials (Church et al., 1994; Cheng and Miceli, 1996).

Although rats and pigeons show similar behaviour on the peak procedure, one qualitative difference between these two species has been reported. When the FI signal is interrupted briefly

and then resumed prior to the FI elapsing, rats act as if they remember the initial duration of the signal and continue timing the signal when it resumes (Roberts, 1981; Meck et al., 1984; Olton et al., 1987). In contrast, pigeons have been reported to act as if they reset their interval clock following the interruption of the signal, and begin timing anew when the signal resumes (Roberts et al., 1989). However, it has been proposed that the occurrence of 'resetting' reported by Roberts et al. (1989) depends upon when during the signal the interruption occurs (Cabeza de Vaca et al., 1994). Cabeza de Vaca et al. proposed a model whereby the accumulated time decays passively during the interruption.

Whether this putative difference between rats and pigeons in the use of working memory during timing is due to differences in the organization of the avian and rodent (or mammalian) nervous systems is of interest to students of both comparative cognition and comparative neuroanatomy. MacPhail (1993) suggests that this behavioural difference indicates a basic difference in the role of the rodent and avian hippocampus in timing behaviour. Rats with transections of the fornix-fimbria, a lesion which disrupts hippocampal function, behave like normal pigeons in the gap procedure; they reset the FI clock after the signal gap (Meck et al., 1984; Olton et al., 1987). That intact pigeons behave like fornix-lesioned rats on gap tests suggests a possible difference in the neuroanatomy of timing between birds and rats.

One objective of the present experiments was to test the generality of several features of timing behaviour observed in pigeons and rats by examining the timing behaviour of chickadees, a species whose timing behaviour has not been investigated. As the passage of time is an important variable in the day to day life of any animal, the timing behaviour of many species should be investigated (Gallistel, 1990). We also tested the generality, within the class Aves, of the phenomenon of clock resetting on gap trials. Chickadees are in the order passeriformes, while pigeons are in the order columbiformes. As these two orders are phylogenetically distinct representatives of the class Aves, observations of similarities in cognitive function in the two species

suggest that the common features may be general within Aves. It should be noted that a difference found in any one experiment or series does not constitute unequivocal support for the existence of a species difference nor a difference between taxa. Each result must be viewed as a single data point in the larger comparative endeavour. Such comparative experiments will make it possible to determine how general timing mechanisms are across species (Lejeune and Wearden, 1991).

2. Experiment 1

We used the peak procedure (Catania, 1970; Roberts, 1981) to quantify the behaviour of chickadees responding on 12.5 and 37.5 s FI schedules of reinforcement. To examine the extent of the similarities among species studied to date, the analysis of the break-run-break pattern of responding performed by Cheng and Westwood (1993) on pigeons was also applied to the resulting data. Part of this analysis is an examination of the correlations between the time of the start, middle, stop, and spread of a run, as well as the average rate of responding during the run. The correlations among these variables can be used to differentiate hypotheses regarding the number of regulating elements present in the timing system. The observation of similar patterns of correlation between species suggests that the same elements, linked in the same manner, are present in the different species' timing mechanisms.

2.1. Method

2.1.1. Subjects

Four wild-caught chickadees were housed individually in wire mesh cages (36 × 36 × 61cm) on an 10:14 L:D cycle (lights on 07:00 h). The birds were fed a diet of insectivorous bird mix supplemented with boiled egg, shredded carrots, peanuts, sunflower seeds, and mealworms (*Tenebrio molitor*). Water with vitamin supplement was available at all times. In the evenings prior to testing days, all food was removed from the birds' cages near light offset and was not available the following day until testing was completed. Birds

were deprived of food overnight plus about 3 h each morning prior to the commencement of testing. Each animal was usually tested three or four times a day, 6 or 7 days a week.

2.1.2. Apparatus

Animals were tested in a cubic wire mesh operant chamber measuring 61 cm on a side. The chamber was located in the room where the chickadees lived, and was not acoustically isolated from the home cages. A modified grain feeder was located in the center of one wall of the chamber. A housing with a small hole in the top surrounded the feeder such that when the grain hopper was up, the subject could access food through the hole in the housing. This feeding hole was 37 cm above the floor of the chamber. The feeder contained sunflower seeds chopped into bits small enough to pass through a No. 10 (2.0 mm) but too large to pass through a No. 12 (1.7 mm) Canadian Standard Sieve. Twelve centimeters above the feeder were two pecking keys, separated by 10 cm, that could be illuminated from behind. A perch was positioned 7 cm under each pecking key, such that the birds could easily reach the key while perching. Several other perches were also available elsewhere in the cage. Water was available at all times on the floor of the chamber. Events were controlled and data were collected by an Apple II computer controlling an SandK Computer Products (Buffalo, New York) interface.

2.1.3. Procedure

Chickadees were first trained to approach and eat from the activated feeder, and then to peck the illuminated right hand key for reinforcement. Once they were pecking and eating reliably, two birds (G1, A) were placed on an FI 12.5 s schedule, and the two other birds (B,D) were trained on an FI 37.5 s schedule. Two types of trials occurred in each session: 15 FI trials in which the first response after the FI was rewarded with 5 s access to the feeder, and three test trials on which the key remained illuminated for 112.5 s and reinforcement was withheld. Test trials were randomly distributed among the total of 18 trials with the constraint that a test trial could not occur during the first four trials of a session, and

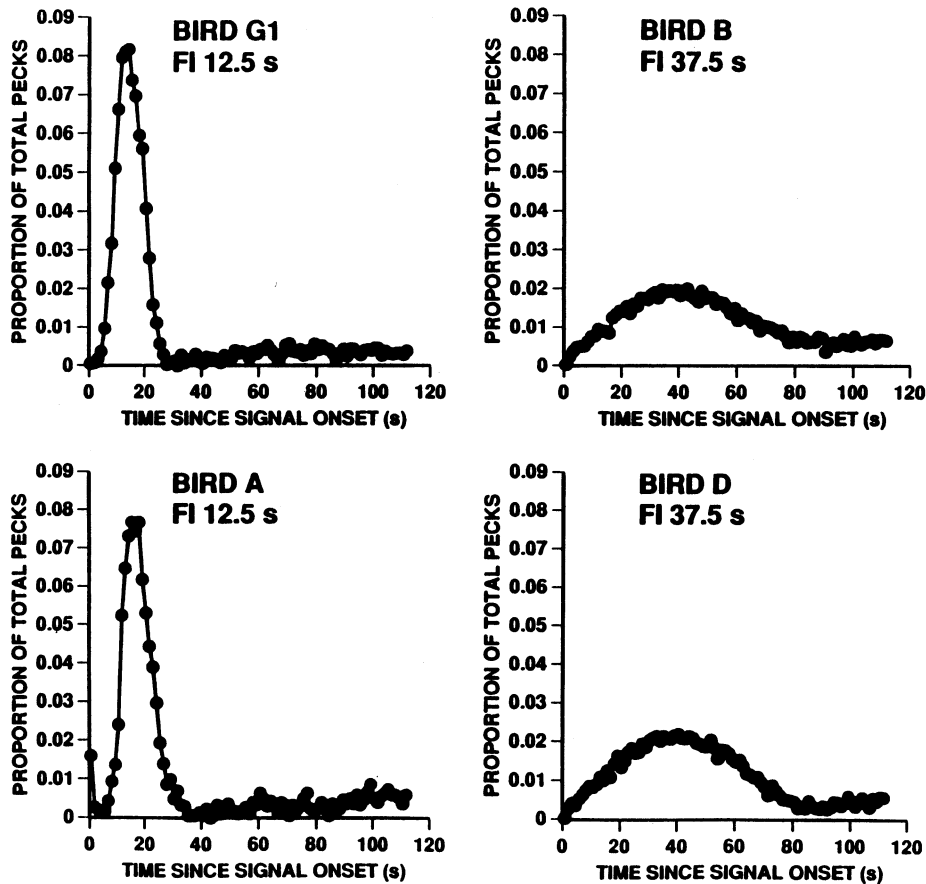


Fig. 1. Summed response distributions of the last 150 empty trials for individual chickadees trained on FI 12.5 (left panels) and FI 37.5 (right panels) in Experiment 1.

two test trials were separated by at least 2 FI trials. Data were collected during the test trials in 1.25 s bins, for 90 bins. The intertrial interval was always 40 s.

The birds were trained for 190 sessions, except for bird B, which died after session 96. Data from the last 50 sessions were collapsed for each bird and the resulting frequency distributions of responses since signal onset were analyzed as described in Cheng and Roberts (1991). Three descriptive statistics result from this analysis: time of the peak rate of responding (peak time), maximum rate of responding (peak rate), and the width of the distribution of responses at half of its height (spread).

2.2. Results

The distributions of responding generated by the four birds are depicted in Fig. 1. As is observed in pigeons and rats, the maximum rates of responding are near the scheduled FI and the spread of the distributions, or error, is larger at the longer FI. The chickadees peaked later, and showed less spread on average than did the pigeons reported in Cheng and Westwood (1993). Calculated peak times, peak rates, and spreads are shown in Table 1, along with values for pigeons trained on an FI 12.5 s schedule from Cheng and Westwood (1993).

Weber's law states generally that the spread, or error of an estimation is proportional to the

Table 1
Peak time, peak rate and spread as a function of species and FI schedule

Group		Peak time (s)	Spread (s)	Peak rate (pecks per min)
Chickadees FI 12.5	G1	14.49	6.54	548.52
	A	17.13	7.04	179.56
	Mean	15.81	6.79	364.04
	D	40.80	27.86	276.59
Chickadees FI 37.5	B	42.02	29.60	273.74
	Mean	41.41	28.73	275.17
Pigeons	Mean	11.60	15.80	189.90

Data on pigeons Cheng and Westwood (1993).

magnitude of the quantity being estimated. In the present case Weber's law predicts that the spread of summed responses for FI 37.5 s birds should be three times larger than the spread for FI 12.5 s birds. This prediction can be tested graphically by plotting each subjects' summed response distributions in a standardized fashion where the x -axis indicates the proportion of peak time and the y -axis indicates the proportion of peak rate. When Weber's law holds, the summed response distributions should lie one on top of another. Birds tested on the FI 37.5 s schedule showed disproportionately more error than did birds tested on the 12.5 s schedule as indicated by the larger spread of these birds on the standardized plot (Fig. 2). A t -test comparing the coefficients of variation (spread divided by peak time) between birds tested on the two schedules was significant ($t(2) = 11.48, p < 0.01$). Thus, in the small sample of birds tested here Weber's law was not supported.

2.2.1. Break-run-break analysis

While summed response distributions on the peak procedure tend to be smooth and Gaussian shaped, individual trials are not. Pigeons (Cheng and Westwood, 1993), rats (Church et al., 1994), and humans (Rakitin et al., 1998) show little or no responding (a break) followed by an abrupt burst of responding (a run) followed by another break. Our break-run-break analysis was conducted using the methods of Cheng and Westwood (1993). Each individual test trial was divided into a run phase and a break phase. The beginning of the run phase was defined as the first

of two consecutive 1.25-s bins containing a response. The break was defined as the first of two consecutive bins, following the onset of a run, in which there was no response. Trials in which a run was detected only after the FI had elapsed were discarded, leaving 85.5% of the empty trials. Five values were calculated from the analysis of each trial. These were the time of the start of the run (start), the end of the run (stop), the middle of the run (middle), the duration of the run (spread), and the average pecking rate during the run (rate).

The break-run-break pattern of responding is shown in Figs. 3 and 4. Table 2 shows means and standard deviations for run-phase variables, and permits comparison with the same measures taken from pigeons performing on FI 12.5 s (Cheng and Westwood, 1993). Consistent with the observation that our chickadees peaked later than did the pigeons of Cheng and Westwood (1993), chickadees started and ended their runs later than did the pigeons. Chickadees' runs were also shorter, consistent with the smaller spread evident in the pooled distributions. Table 3 depicts mean correlations of run-phase variables along with the results of Cheng and Westwood (1993) for pigeons on the FI 12.5 s schedule. One way to examine the similarity of patterns across run phase variables is to look at the correlations of the sets of correlations reported in Table 3. For the sets of correlations in Table 3, pigeons correlated with chickadees on FI 12.5 s by 0.951, pigeons correlated with the chickadees on FI 37.5 s by 0.981, and the two chickadee data sets correlated by 0.984.

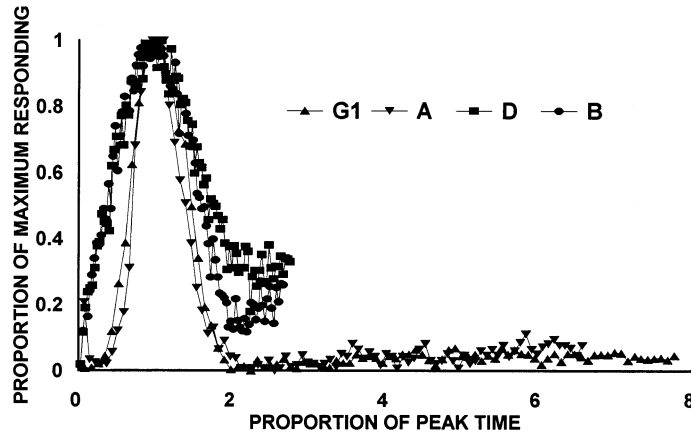


Fig. 2. Summed response distributions plotted relative to the peak time for individual chickadees on empty trials in Experiment 1.

Figs. 5 and 6 show theoretical individual trial curves if responding rose and fell according to a Gaussian distribution on individual trials for FI 12.5 and 37.5 s, respectively. The pattern for the subjects' responding in Experiment 1 can be compared to this standard and also to a horizontal line starting at the onset of the signal to see if the subjects' responding was similar to either of these theoretical curves. A computer program similar to that used by Cheng and Westwood (1993) generated 200 Gaussian shaped trials for each interval based on the formula for a Gaussian distribution:

$$y = \frac{\exp[-(x - M)^2/2s^2] \times H}{s/(2\pi)^{1/2}}$$

where M is the mean, s is the standard deviation and H is the height. Parameters were chosen such that the theoretical distributions had similar values for run phase variables for each condition. M , H and s varied randomly around these parameters on a trial by trial basis. Correlations of these computer generated run phase variables are presented in Table 3. The chickadees in the FI 12.5 s, and FI 37.5 s conditions' correlations correlated with their respective simulations by 0.809 and 0.634.

2.3. Discussion

The timing behaviour of chickadees is similar to that of both pigeons and rats. Tested using the

peak procedure, chickadees show peaks of responding near the scheduled FI, and the spread of the distribution of responses is larger at the longer FI. Although the chickadees in this study tended to peak later and show less spread than did pigeons trained on the same schedule, this may be an artifact of the small sample size as well as possible differences in procedure such as the extensive training our subjects received. These same reasons may explain the lack of superposition shown in Fig. 2 and the differences when *c.v.s* were compared.

Like pigeons and rats, chickadees showed abrupt bursts of responding on individual trials, rather than the steady increases and decreases in responding suggested by the averaged data shown in Fig. 1. The smooth curves found in Fig. 1 result from averaging discontinuous behaviour across trials, and do not represent behaviour on individual trials. The averaged data are more accurately described as indicating the probability of responding, rather than rate of responding. Correlations of start times, stop times, middles, spreads, and rates for these bursts of activity show remarkable resemblance to those previously reported for pigeons. The similar pattern of correlations is consistent with the view that the same elements are present in the timing mechanisms of pigeons and chickadees, and that they are interconnected in the same manner. Likely, models such as those proposed by Church et al. (1994) or

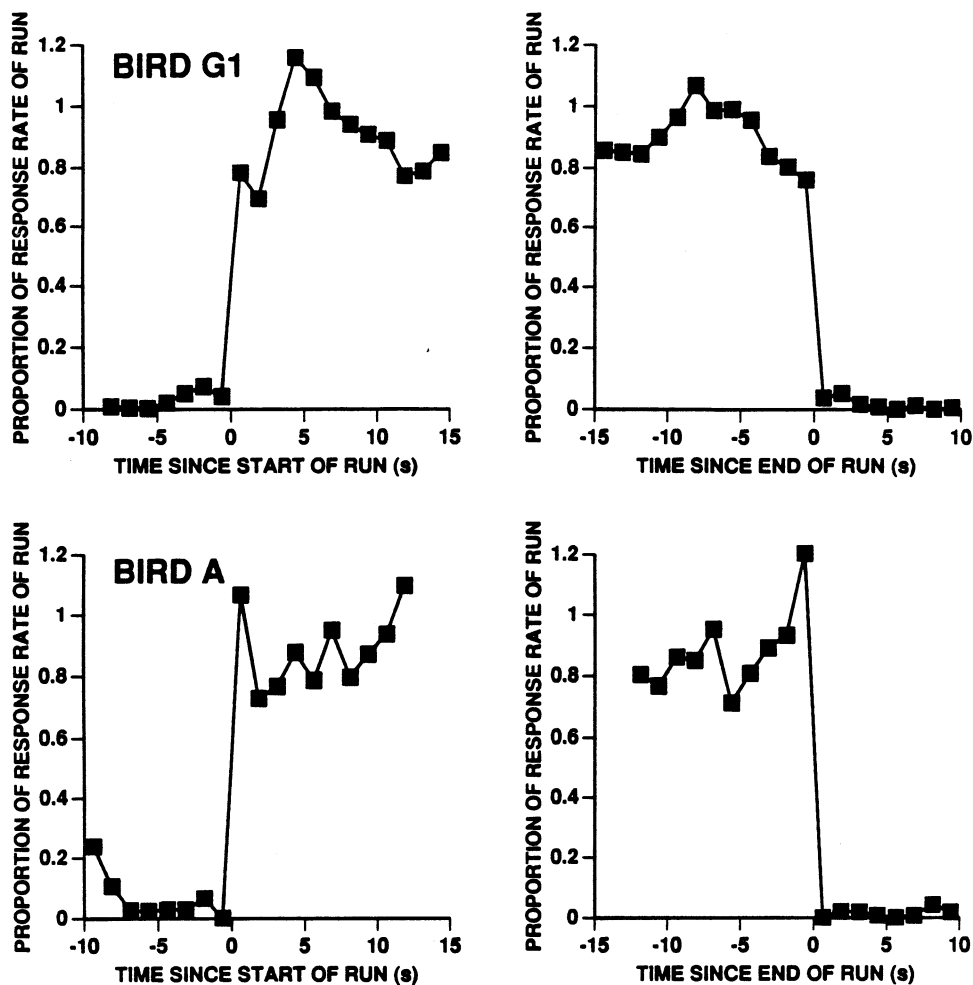


Fig. 3. Rate of responding expressed as a proportion of the average rate of responding during the run phase, as a function of time before and after the start of the run (left panels), and time before and after the end of the run (right panels) for individual chickadees trained on FI 12.5 s.

Cheng and Miceli (1996) can account for these data.

While the pattern of correlations are similar between black-capped chickadees and pigeons, the species differ in one regard in their trial-by-trial behaviour. Experiment 1 found an exceptionally high rate of responding in chickadees just after the start of a run, and just before the end of a run (Figs. 2 and 3). Cheng and Westwood (1993) reported no such burst in their analysis of single trials in pigeons, and Church

et al. (1994) did not report such a burst in their analysis of rat data. Cheng and Miceli (1996), however, found this anomalous pattern with three different FI's in pigeons, and attributed it to the method of analysis used. The method of analysis here was that used by Cheng and Westwood, and not the one used by Cheng and Miceli. It is not clear what the cause of the bursts is, but we suspect that it still results from an artifact of the method of analysis when applied to the chickadees.

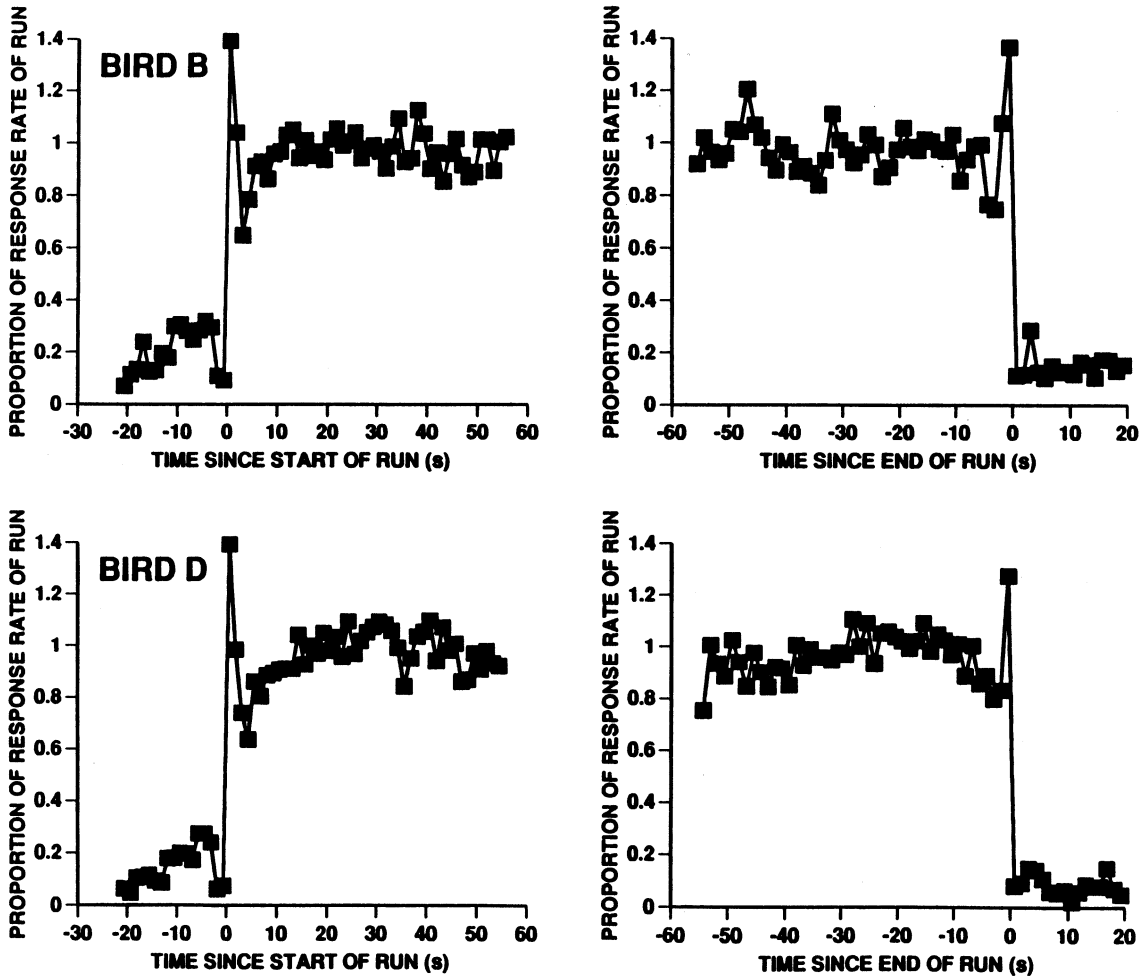


Fig. 4. Rate of responding expressed as a proportion of the average rate of responding during the run phase, as a function of time before and after the start of the run (left panels), and time before and after the end of the run (right panels) for individual chickadees trained on FI 37.5 s.

3. Experiment 2

The pigeons studied by Roberts et al. (1989) appeared to 'reset' their internal clocks when a gap interrupted the FI signal. This resetting phenomenon is not observed in rats unless the function of the hippocampal system is disrupted by fornix lesion (Olton et al., 1987). In this experiment we presented chickadees with test trials in which the FI signal was interrupted briefly. Chickadees represent a different order of birds than do pigeons, and thus an independent sample from the

class Aves. If chickadees show the same tendency to reset the clock observed previously in pigeons, the argument for the generality of this resetting phenomenon within the class Aves would be supported.

3.1. Method

Three of the four birds (G1, A, D) used in Experiment 1 were used for this experiment. They were housed and maintained as in Experiment 1. There were no changes in equipment from that used in Experiment 1.

Table 2
Means and standard deviations across trials of the run phase variables

Variable	FI 12.5				FI 37.5	
	Pigeon		Chickadee		Chickadee	
	Mean	S.D.	Mean	S.D.	Mean	S.D.
Start	5.62	2.33	10.07	2.02	17.85	8.34
Stop	18.88	3.17	21.59	3.28	65.76	13.54
Middle	12.25	2.29	15.20	2.20	41.18	9.64
Spread	13.27	3.14	11.51	3.20	47.91	11.6
Rate	1.85	0.33	2.45	0.46	1.88	0.39

Standard deviations across trials is calculated separately for each subject and then averaged across subjects. Spread refers to duration in seconds, and rate is responses per second. Data on pigeons from Cheng and Westwood (1993).

Animals were tested on the same daily schedule as in Experiment 1. All birds were trained on FI 12.5 s for 81 sessions, each with 15 regular FI and three test trials. Starting with session 82 the birds received sessions with three normal test trials identical to those used during training, in alternation with sessions with three ‘gap’ test trials, in which the FI signal was interrupted. On gap trials the keylight was illuminated for 6.25 s, extinguished for 6.25 s, and then illuminated again for 100 s. Each test trial is therefore comprised of 90 bins of 1.25 s each. Each subject participated in 30 sessions each of regular and gap test trials, yielding a total of 90 tests per condition per bird. A 40 s ITI was used as in Experiment 1.

3.2. Results

The chickadees showed a pattern of responding consistent with resetting after the gap (Fig. 7). If animals continue to time the FI signal after the gap, peak times for gap trials should be 6.25 s later (the duration of the gap) than those recorded on control trials. If the birds reset their interval clocks and begin timing anew after the gap, peak times for gap trials should occur 12.5 s later than they do on control trials. The mean peak times on control and gap trials reported in Table 4 support the account that the birds reset their clocks after the gap.

3.3. Discussion

The behaviour of chickadees tested on the gap procedure is similar to that observed previously in pigeons (Roberts et al., 1989) and in rats with fimbria–fornix lesions (Meck et al., 1984; Olton et al., 1987): Chickadees reset the interval clock following a gap in the FI signal. The observation of this result in both pigeons and chickadees suggests that the failure to use working memory in such gap tests is a general phenomenon among birds. It should be noted that the other experiments reviewed were quantitatively different from Experiment 2 (e.g. placement of the gap). For this reason, and in light of recent work by Cabeza de Vaca et al. (1994) discussed below, our ‘resetting’ result should be regarded with caution.

On gap trials, chickadees had a wider spread and a lower rate than on normal empty trials. The gap may have provided a discriminative signal that reward was not forthcoming. This must have been a time based signal, as the ITI was also a gap in the signal, albeit longer. In other words, the long ITI was seen as an interval between trials, after which the signal would appear and the subject would respond as if food was forthcoming. On the other hand, the gap came after a short presentation of the signal, and was shorter than the ITI. As gaps never occurred on FI trials, the gap signalled that no reward was forthcoming.

Table 3

Mean correlations between the run phase variables for pigeons in Cheng and Westwood (1993), chickadees in this study and for computer generated Gaussian individual trials

Correlation	Pigeon		Chickadee		Computer	
	FI 12.5	FI 12.5	FI 12.5	FI 37.5	FI 12.5	FI 37.5
Start–stop	0.380	0.352	0.526	0.702	0.821	
Start–middle	0.765	0.713	0.798	0.949	0.954	
Start–spread	–0.357	–0.284	–0.118	–0.340	–0.277	
Stop–middle	0.880	0.905	0.931	0.926	0.955	
Stop–spread	0.714	0.792	0.777	0.431	0.321	
Middle–spread	0.307	0.460	0.496	0.057	0.026	
Start–rate	0.036	–0.288	0.009	–0.122	–0.236	
Stop–rate	–0.100	–0.171	0.103	0.166	0.297	
Middle–rate	–0.050	0.003	0.079	0.027	0.034	
Spread–rate	–0.124	0.036	0.116	0.374	0.892	

Data on pigeons from Cheng and Westwood (1993).

4. General discussion

In Experiment 1, black-capped chickadees trained on the peak procedure with FI's of 12.5 and 37.5 s showed peak response times at their respective FI's. Single trials were characterized by a burst of responding before the FI, which continued until after the FI. When a gap was introduced early in the FI signal in Experiment 2 the chickadees' peak time shifted in a manner consistent with the reset hypothesis.

The timing behaviour of pigeons, chickadees, and rats is remarkably similar. However, rats and

birds may differ in their use of working memory as indicated by their behaviour on gap trials. This pattern of striking similarity punctuated by a notable difference provides an exciting challenge to comparative psychologists and neuroanatomists.

There was much similarity in the summed distributions of pecks during empty trials found in rats, pigeons and the chickadees in our study. The distributions in our study were roughly Gaussian (Experiments 1 and 2), a longer FI led to a larger spread (Experiment 1) and a larger rate was found with a smaller FI (Experiment 1). The results of the break-run-break analysis carried out on our

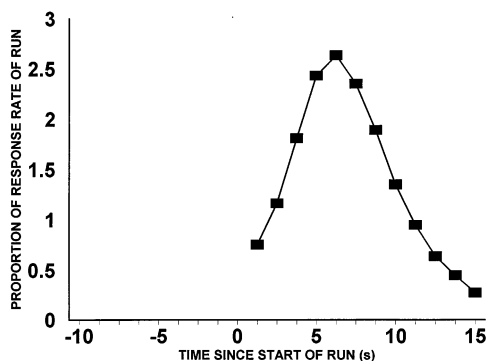


Fig. 5. Rate of responding expressed as a proportion of the average rate of responding during the run phase, as a function of time before the start of a run for computer simulated Gaussian single trials at FI 12.5 s.

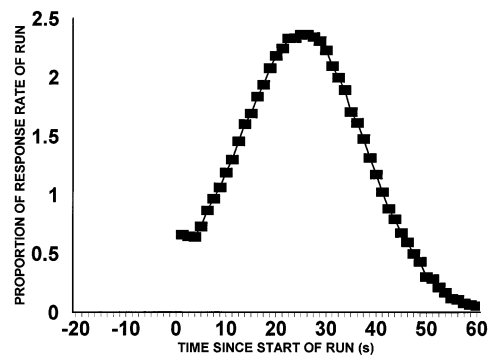


Fig. 6. Rate of responding expressed as a proportion of the average rate of responding during the run phase, as a function of time before the start of a run for computer simulated Gaussian single trials at FI 37.5 s.

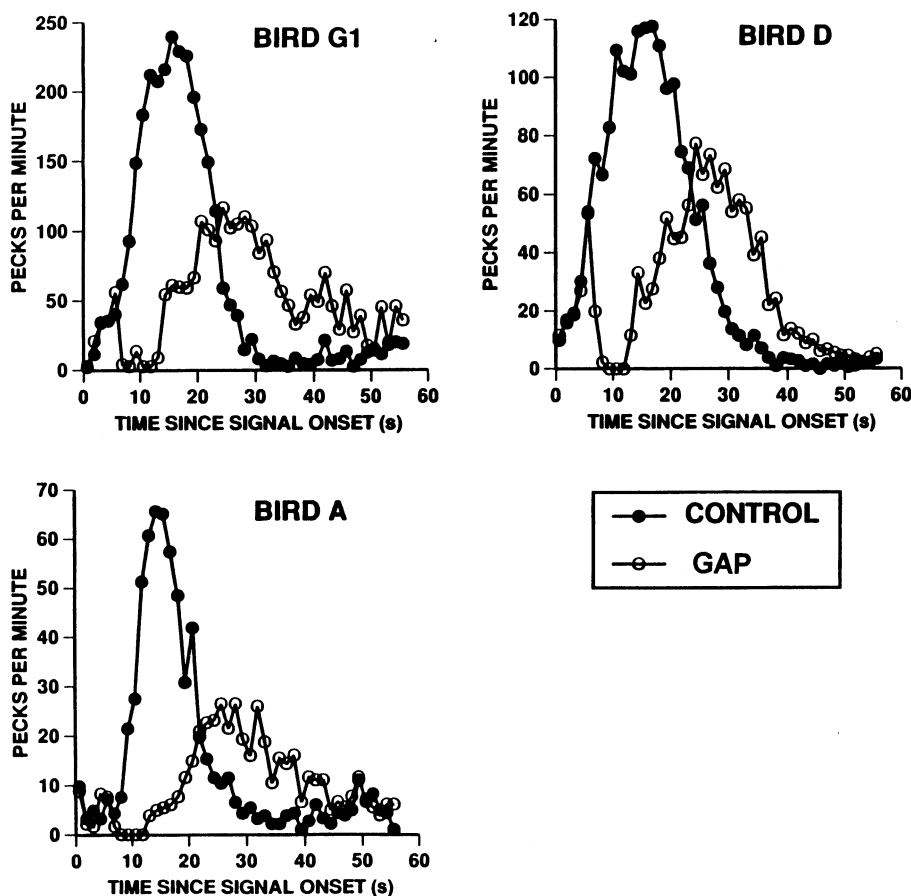


Fig. 7. Summed response distributions for individual chickadees on control and gap trials in Experiment 2.

data also show a stunning similarity in trial-by-trial behaviour between rats, pigeons, and chickadees. The patterns of correlations between the various run phase variables (Table 3) are quite similar to those reported by Cheng and Westwood (1993) and Cheng and Miceli (1996). These similarities show that chickadees time an interval using similar mechanisms to those used by other

species. While we have not carried out any modelling on these data, it seems likely that models similar to those used by Cheng and Miceli (1996) and Church et al. (1994) would be suitable.

One difference between the chickadees (this study) and pigeons (Roberts et al., 1989) on the one hand and rats (Roberts, 1981) on the other, is that the birds behaved as if they had reset their clocks during a gap, whereas rats behaved as if they had stopped their clocks during the gap and restarted when the signal restarted. Recently, Cabeza de Vaca et al. (1994) presented a compelling reinterpretation of the pigeons' performance. They tested pigeons on a task similar to that used by Roberts et al., except that the gap was placed in many different positions during the signal. They found that if the timeout was early in

Table 4

Mean peak rate, spread and response rate as a function of trial type in Experiment 2

Trial type	Peak time (s)	Spread (s)	Rate (pecks per min)
Control	15.62	7.99	203.38
6.25 s Gap	27.74	14.74	94.89

the signal resetting like behaviour was the result, replicating Roberts et al. If the timeout was later in the empty trial, however, the data were more consistent with stopping the clock. They concluded that a continuous decay model of timing was more appropriate than either a reset or a stop-retain model. This notion fits well with other data on timing, such as the subjective shortening effect found by Spetch and Wilkie (1983). In Spetch and Wilkie's paradigm, pigeons were presented with a stimulus of a given duration (either 'short' or 'long') and, after a delay interval, they were required to peck one keylight if they remembered a long interval, and another for a short interval. When the delay interval was increased pigeons tended to choose the short key an inordinate amount of the time. This 'choose short effect' was explained by Spetch and Wilkie (1983) with a 'subjective shortening model'. Basically, the model says that as the delay interval increases the remembered duration undergoes a gradual foreshortening. This decay of memory for a duration fits nicely with Cabeza de Vaca et al.'s (1994) hypothesis. In fact, Roberts et al.'s (1989) data are also suggestive of a decay process. When the timeouts used by Roberts et al. decreased, the results fell somewhere between those predicted by the reset and the stop hypotheses (Roberts et al., 1989, Fig. 7).

There is still a difference between the data from rats and birds studied so far that requires explanation, even if one accepts the decay hypothesis of Cabeza de Vaca et al. (1994). Roberts' (1981) rats showed little or no decay using parameters similar to those that caused pigeons and black-capped chickadees to show complete decay. What differences in the organization of timing mechanisms, and the psychological process they serve, can account for the fact that birds behave like fimbria-fornix lesioned rats on gap trials? The possibility that birds lack the equivalent pathways in the fornix is unlikely. Casini et al. (1986) demonstrated the existence of an avian equivalent of the mammalian postcommissural fornix, and previous research had demonstrated the existence of projections similar to the precommissural fornix (Krayniak and Siegel, 1978). Alternatively, the avian hippocam-

pal complex may not be as involved in timing behaviour, although it is in rodents. Determination of whether disruption of the hippocampal system in birds results in a decrease in the remembered duration of a previously trained FI schedule, as it does in rats (Olton et al., 1987) would constitute one test of the involvement of the hippocampus in timing in birds.

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