

Oscillations following periodic reinforcement

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ABSTRACT

Three experiments examined behavior in extinction following periodic reinforcement. During the first phase of Experiment 1, four groups of pigeons were exposed to fixed interval (FI 16 s or FI 48 s) or variable interval (VI 16 s or VI 48 s) reinforcement schedules. Next, during the second phase, each session started with reinforcement trials and ended with an extinction segment. Experiment 2 was similar except that the extinction segment was considerably longer. Experiment 3 replaced the FI schedules with a peak procedure, with FI trials interspersed with non-food peak interval (PI) trials that were four times longer. One group of pigeons was exposed to FI 20 s PI 80 s trials, and another to FI 40 s PI 160 s trials. Results showed that, during the extinction segment, most pigeons trained with FI schedules, but not with VI schedules, displayed pause–peck oscillations with a period close to, but slightly greater than the FI parameter. These oscillations did not start immediately after the onset of extinction. Comparing the oscillations from Experiments 1 and 2 suggested that the alternation of reconditioning and re-extinction increases the reliability and earlier onset of the oscillations. In Experiment 3 the pigeons exhibited well-defined pause–peck cycles since the onset of extinction. These cycles had periods close to twice the value of the FI and lasted for long intervals of time. We discuss some hypotheses concerning the processes underlying behavioral oscillations following periodic reinforcement.

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1. Introduction

The fixed-interval (FI) reinforcement schedule is probably the simplest procedure that can be used to study the behavioral effects of periodic reinforcement (Skinner, 1938). In a FI schedule T -seconds long (FI T s) a reinforcer follows the first response emitted after T s have elapsed since the previous reinforcer. At the steady state performance is characterized by a post-reinforcement pause roughly proportional to T , the schedule parameter (Richelle and Lejeune, 1980), followed either by a constant rate of responding (Schneider, 1969) or by an accelerated rate of responding (Dews, 1978). In the cumulative record, these two types of performance yield the distinctive break-and-run and scalloping patterns, respectively.

How does behavior change if the reinforcers are discontinued but all other procedural features remain unchanged? In other words, what is extinction like following FI training? The question is important because the animal may reveal during extinction new, long lasting, and perhaps unsuspected effects of periodic reinforcement – in much the same way as the duration of the post-reinforcement pause already reveals during condi-

tioning some of these effects. Thus, behavior in extinction may help us better characterize what animals learn under periodic reinforcement.

Interestingly, there are several descriptions of extinction following FI training but they are not all consistent. On the one hand, following Ferster and Skinner (1957), Reynolds (1968) states that “after reinforcement on a FI schedule, responding during the first interval of extinction is normal, except that the high terminal rate continues beyond the end of the interval, when reinforcement would have occurred. In a short time, responding ceases abruptly. Then, after a pause, there is a period of acceleration, followed by the original terminal rate, which is again followed by an abrupt end to responding. This pattern of pause, respond, accelerate, and abruptly stop, whose origins can be seen in the scallop of the maintained performance, continues through extinction. The pauses become longer and the periods of responding become shorter as the rate of responding approaches zero” (p. 76). The description suggests that, at least early in extinction, behavior is characterized by pause–peck cycles whose duration is closely related to the FI parameter or, in other words, that the animal’s behavior oscillates with the period of the oscillation being close to the FI parameter. To corroborate this interpretation, note that Reynolds even draws stylized cumulative records in extinction showing scallops similar to, but slightly longer than the scallops observed during reinforcement (see Reynolds, 1968, Fig. 6.5). In a similar vein, a popular laboratory manual of

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the time (Reese, 1964) concluded that, after prolonged FI training, “the [cumulative] extinction curve may contain long scallops appropriate to the interval” (p. 72, italics added).

On the other hand, Gallistel (1990, p. 297) describes extinction following FI training as follows: “During extinction following an FI schedule of reinforcement, the pigeon does *not* show periodic FI scallops. When the first reinforcement fails to appear, the pigeon goes on pressing at a very high rate for an interval three or four times longer than the fixed interval used, pauses for an unpredictable amount of time, resumes pressing with another burst much longer than the fixed interval, and so on” (italics added). The author concludes that behavior in extinction indicates that during training pigeons form “aperiodic” (sic) representations of the temporal interval since the last reinforcement. According to this description, behavior during extinction has few if any similarities with behavior during conditioning.

Conspicuously missing from these contrasting descriptions are any references to systematic studies supporting them. Reynolds (1968) does not cite any studies of extinction following FI training; Gallistel (1990) and Reese (1964) refer to one cumulative record from Ferster and Skinner (1957); and the textbooks that included stylized cumulative records similar to Reynolds’ (e.g., Blackman, 1974, Fig. 10; Domjan, 1998, Fig. 6.4; Millenson and Leslie, 1979, Fig. 5.15; Walker, 1996, Fig. 4.4) do not mention any empirical evidence either. Recently, however, a few studies have examined behavior in extinction following periodic reinforcement.

Machado and Cevik (1998) exposed pigeons to FI 40 s or FI 80 s schedules for approximately 60 sessions of 50 trials each. Then, for the next 15 sessions, the pigeons experienced between 10 and 40 FI trials followed by extinction for the remainder of the session (see Bullock, 1960, for a similar procedure). Thus, each session included an initial reconditioning segment and a final re-extinction segment; the transition from the two segments was unpredictable. Results showed that, during the extinction segment of the first session, most pigeons pecked for an interval 10 times longer than the FI parameter. Two out of six pigeons started to produce pause–peck oscillations by the end of the first session, but the other birds produced such oscillations only after two or three sessions. When pause–peck oscillations were clearly present, their periods were slightly longer than the FI parameter. Across sessions, the oscillations started earlier during the extinction segment.

Crystal and Baramidze (2006) conducted a similar study in which rats were trained with FI 48 s, 96 s or 192 s schedules before they were exposed to one long extinction segment. The authors reported that the behavior observed during extinction was similar to the behavior observed during conditioning. That is, response rate in extinction oscillated with a period close to the FI parameter. Note that in these two studies, as well as in any other study with FI schedules, the response rate oscillations observed during conditioning are driven by the stimulus changes that accompany food delivery and the onset of the next trial (e.g., in rats, the pellet dispenser is activated and the lever may be retracted and then reinserted; in pigeons, the houselight and keylight are turned off, the hopper is activated, and the houselight and keylight are illuminated again). However, the response periodicities observed in extinction are not driven by any external stimulus changes. They are endogenously generated.

In a different line of research, Kirkpatrick-Steger et al. (1996) reported unexpected oscillations in the peak interval procedure. In this procedure, FI or food trials are randomly interspersed with longer, unreinforced trials, also designated as peak interval (PI) trials. After an intertrial interval (ITI), a cue such as a sound for rats or a keylight for pigeons is presented and then, if the trial is a FI trial, the first response after the interval is reinforced, the cue is turned off, and the next ITI starts; if the trial is a PI trial, then at the end of

the interval the cue is simply removed and the next ITI starts. The typical result from the peak procedure is that, during the PI trials, the average response rate curve increases from the beginning of the trial ($t=0$ s) until the time food is primed on FI trials (at $t=T$ s, say), then it decreases again, sometimes asymmetrically (e.g., Catania, 1970; Church et al., 1991; Roberts, 1981).

Using pigeons, Kirkpatrick-Steger et al. (1996) found that, when the PI trials were four times longer than the FI trials, average response rate during the PI trials increased from $t=0$ s until $t=T$ s, decreased until $t=2T$ s, increased again until $t=3T$ s and finally decreased until the end of the trial at $t=4T$ s. That is, the average response rate curves showed two peaks, the first at T s, the FI parameter, and the second at $3T$ s. Four peaks were obtained when a second type of PI trials, eight times longer than the FI, was occasionally added to a FI T s–PI $4T$ s peak procedure. According to the authors, these results suggest the presence of an endogenous oscillator that was entrained by the periodic reinforcers. Surprisingly, with other ratios of FI to PI trial durations, oscillations were less reliable and the average response rate curves yielded not a second peak but a ramp, that is, a monotonic increase in response rate from $t=2T$ s till the end of the trial.

Sanabria and Killeen (2007) attempted to replicate Kirkpatrick-Steger et al.’s (1996) results, both with rats and pigeons, but they always found a ramp instead of a second peak in the average response rate curve (see also Church et al., 1991). The authors attributed the ramp to an anticipation or expectation of the next reinforcer (as if the animals had timed across successive trials), and attributed the difference in results between the two studies to procedural variations in the nature of the time markers. Specifically, in both experiments the houselight was lit during the ITI but then, when the trial started with the illumination of the keylight, the houselight was turned off in Sanabria and Killeen’s experiment but remained on in Kirkpatrick-Steger et al.’s experiment. Sanabria and Killeen argued that double peaks or oscillations may require more diffuse or less salient time markers.

The preceding studies raise several questions concerning extinction after periodic reinforcement, questions that were addressed in the three experiments reported below. First, when do oscillations occur after FI training? Crystal and Baramidze (2006) reported oscillations in rats immediately after the onset of extinction. Machado and Cevik (1998) reported oscillations in pigeons also during the first session, but only for a minority of subjects and after a long period of uninterrupted pecking; for most subjects, oscillations occurred only after a few sessions of reconditioning and re-extinction. However, it is possible that most pigeons in Machado and Cevik’s (1998) study did not show oscillations during the first session simply because the extinction segment was too short. Unlike rats, most pigeons may need longer segments of extinction before they start to pause and peck and pause again. The hypothesis can be tested by lengthening substantially the extinction segment of the first session.

Second, how much of the oscillatory behavior depends on the average and variance of the inter-reinforcement interval? One way to answer the question is to compare extinction following a FI T s schedule with extinction following a variable interval (VI) T s schedule. The average inter-reinforcement interval will be approximately the same in the two cases, but only in the former will the reinforcer be periodic (variance of inter-reinforcement intervals close to zero). More generally, behavior in extinction after a VI schedule may function as a control or a baseline against which behavior in extinction after the corresponding FI schedule may be compared. No previous study included such control.

Third, which conditions engender clearer or more reliable oscillations and why? Consider the studies with pigeons. Machado and Cevik found pause–peck cycles in extinction but these cycles

were not always clearly periodic. In addition, there was substantial variation both within and between subjects. In contrast, Kirkpatrick-Steger and collaborators found extremely clear oscillations when the FI and PI trials were in a 1-to-4 ratio, so clear in fact that the double peaks in the response rate curves were preserved despite substantial averaging (across sessions for the same pigeon and then across pigeons). The preservation of the peaks after averaging indicates that the different subjects had their two peaks at approximately the same times into the trial; the average response rate curves were in phase.

Kirkpatrick-Steger et al.'s results suggest that oscillatory behavior may be more reliable in the peak procedure than in FI schedules. Why? Perhaps because for behavior to oscillate the animal needs to learn not only when to start responding, which learning takes place during the FI trials common to both procedures, but also when to stop responding, which learning takes place during the empty trials present only in the peak procedure. It may also be the case that frequent alternation between reinforced and unreinforced trials improves the learning and thereby increases the reliability of oscillations in extinction.

The foregoing hypothesis could explain the individual differences reported by Machado and Cevik (1998). If in order to learn to stop responding different birds need different degrees of exposure to extinction segments, or different degrees of alternation between reinforcement and extinction segments, then some birds will oscillate at the end of the first extinction segment, whereas other birds will oscillate only after several sessions of reconditioning and re-extinction.

However, the foregoing hypothesis fails to explain why Sanabria and Killeen (2007) found a ramp and not a second peak. As we mentioned before, these authors pointed to differences in the time markers to account for the discrepancy, but other accounts are possible. For example, the ramp itself could be the beginning of a (delayed) second peak, which would not be seen simply because the end of the empty trial prevented it. That is, with relatively short empty trials the animals would not have the opportunity to reveal the second response rate cycle. The ramp could also be due to the averaging of response rate oscillations out of phase. If any of these hypotheses is correct, then two consequences follow. First, differences in the time markers could be responsible not for the presence or absence of rate peaks or, more generally, rate oscillations per se, but for their immediate or delayed onset. And second, lengthening the PI trial substantially and looking at cumulative response records (i.e., without averaging response rate curves) should reveal not only a second, but also a third and a fourth cycle, that is, reliable behavioral oscillations.

Below we report three experiments designed to study in greater detail the phenomenon of behavioral oscillations in extinction after periodic reinforcement. Experiments 1 and 2 used Machado and Cevik's (1998) design, but added adequate VI control groups. During the first phase of both experiments, pigeons were trained with FI or matching VI schedules. During the second phase, pigeons were exposed to an unpredictable number of food trials followed by an extinction segment. The two experiments differed in the length of the extinction segment. In Experiment 1, the extinction segment was relatively short, such that session length remained approximately constant throughout the experiment, whereas in Experiment 2 the extinction segment was substantially longer. At issue were the effects on the behavioral oscillations of the average and variance of the inter-reinforcement interval (FI vs. VI groups), and whether oscillations occur reliably during the first session provided the extinction segment is sufficiently long (Experiment 1 vs. Experiment 2). Finally, Experiment 3 was conceptually similar to Experiments 1 and 2, but instead of FI schedules it used the peak procedure. In the first phase of the experiment, pigeons were

trained with the usual peak procedure, as in Kirkpatrick-Steger et al.'s (1996) and Sanabria and Killeen's (2007) studies. In the second phase, each session included an extinction segment, which started at an unpredictable moment and lasted until the end of the session. Note that the extinction segment is in every respect equal to a very long PI trial. The issues under consideration were whether reliable oscillations, similar to those reported by Kirkpatrick-Steger and collaborators, occur when the animal has ample opportunity to display them (which may not have been the case in Sanabria and Killeen's study), and whether the peak procedure engenders clearer oscillations than the FI schedules (Experiment 3 vs. Experiments 1 and 2). The results from the three experiments will improve our understanding of the multiple effects of periodic reinforcement such as the presence of behavioral oscillations in extinction.

2. Experiment 1: short extinction

The experiment tried to reproduce and extend the results obtained by Machado and Cevik (1998). In that study, the three pigeons that were exposed to a FI 40-s schedule showed clearer oscillations in extinction than the three pigeons that were exposed to a FI 80-s schedule. These results suggest that oscillations may be more reliable with shorter FIs. Hence, in Experiment 1, we exposed one group of pigeons to a FI 48-s schedule and another to a FI 16-s schedule. The former group attempted to replicate the data from the FI 40 s group in Machado and Cevik's (1998) study, and the latter group attempted to determine whether oscillations are effectively clearer with a shorter FI.

Experiment 1 also attempted to assess the effects, if any, of the average and variance of the inter-reinforcement interval. To that end, two additional groups of pigeons were included in the study, one exposed to a VI 48-s schedule, and the other to a VI 16-s schedule. The VI control groups are important also for a methodological reason. Because there is no simple way to quantify response rate oscillations, we used two distinct, and hopefully convergent, approaches, the visual inspection of cumulative records and power spectra yielded by a Fourier transform analysis of the rate data (see Section 2.1.4 below). The interpretation of cumulative records or power spectra remains to some extent subjective, but one way to reduce the subjectivity is to compare the results from the FI groups against the baseline provided by the results from the matching VI groups.

2.1. Materials and methods

2.1.1. Subjects

Sixteen naive pigeons (*Columba livia*) participated in the experiment. The birds were housed in individual home cages with water and grit continuously available. During the experiment the birds were kept at 80% of their free-feeding body weight. The pigeon colony remained in a 13 h:11 h light:dark cycle, with lights on at 8:00 a.m.

2.1.2. Apparatus

Four standard Lehigh Valley® chambers for pigeons (34 cm × 30.5 cm × 34 cm) were used. The front panel of each chamber contained three response keys 2 cm in diameter, centered on the wall 22 cm above the floor and 8 cm apart, center to center. The central key was illuminated from behind with a red light. Directly below the center key and 4 cm above the floor was the 6 cm × 7 cm hopper opening. A 7.5-W white light illuminated the mixed grain when the hopper was activated. On the back of the chamber, another 7.5-W houselight provided general illumination. An outer box equipped with a ventilating fan enclosed the experimental chamber and provided air circulation and masked

extraneous noise. A personal computer controlled all experimental events and recorded the data.

2.1.3. Procedure

The pigeons learned to peck the central key, illuminated with red light, in 3–5 sessions of hand shaping. Afterwards, they received three 60-trial sessions of continuous reinforcement and then the experiment began. It was divided into Phase 1 (conditioning) and Phase 2 (extinction).

2.1.3.1. Phase 1. The pigeons were assigned randomly to four groups of four birds each, FI 16 s, VI 16 s, FI 48 s, VI 48 s. During the experiment, one pigeon from the VI 16 s group became ill and was removed from the experiment. Each session comprised 50 trials and each trial was as follows. At trial onset, the houselight was turned on and the center key was illuminated with red light. The first peck after the interval elapsed turned off the keylight and houselight and raised the food hopper. During the first three sessions, the hopper duration was adjusted for each bird to minimize extra-session feeding (final durations ranged from 2 s to 5 s). The number of sessions varied across birds from 60 to 70. By then, visual inspection of the post-reinforcement pauses and average rate curves revealed no systematic changes across sessions.

2.1.3.2. Phase 2. Each session, still 50 trials long, started with a reinforcement segment and ended with an extinction segment. Specifically, the first trials were equal to the reinforced trials of Phase 1. Their exact number varied randomly across sessions, from a minimum of 10 to a maximum of 40. This means that the extinction segment began between trials 11 and 41 inclusive, and lasted for a duration corresponding to the trials left. To illustrate, if the last reinforced trial of a pigeon in the VI 48 s group occurred on trial 20, then its extinction segment lasted for 1440 s, the duration of 30 trials of 48 s each. This algorithm, used to compute the duration of the extinction segment, insured that total session duration remained approximately constant throughout the experiment. It is critical to note that during the extinction segment the keylight and the houselight remained illuminated and, therefore, no cue signaled either the beginning or the end of the trials during extinction. Phase 2 lasted 15 sessions.

2.1.4. Data analysis

The analysis followed two approaches. One, more qualitative, was the visual inspection of cumulative records in which we looked for well defined, repeating scallops or break-and-run patterns, the signature of oscillatory behavior. Another, more quantitative, was a discrete Fourier transform (DFT) analysis of the response rate data. The DFT is a useful technique to reveal the relative strengths of any periodic components in the data. It may be conceived as an algorithm that transforms an input sample defined in the time domain into an output sample defined in the frequency domain. In Experiment 1, the input consisted of blocks of response rate data, with rate defined as the number of responses produced during successive 2 s bins (for the 16-s groups) or 6 s bins (for the 48-s groups). The exact number of bins in each block depended on whether it was an extinction block, with data from the extinction segments, or a reinforcement block, with data from the reinforcement trials, but the general rule was that each block should represent approximately 10 trials (i.e., 160 s for the 16-s groups and 480 s for the 48-s groups). The extinction blocks were always 80 bins long, and therefore they represented exactly 160 s or 480 s. The number of bins in the reinforcement blocks varied. For the FI groups, it was always slightly greater than 80 because 10 reinforcement trials lasted slightly more than 160 s or 480 s; for the VI groups, the

number of bins equaled 80 only on the average because 10 reinforcement trials lasted sometimes more and sometimes less than 160 s or 480 s. Finally, each block was linearly detrended (i.e., the least-squares linear fit to the data was subtracted from the data) before submitting it to the DFT analysis. By removing systematic (linear) increases or decreases in response rate, detrending facilitates the analysis of the fluctuations in the data, in much the same way as plotting residuals facilitates regression analysis. No windowing function was used.

The output of the DFT analysis yielded a vector of complex numbers, c_j , related to the amplitudes of the (different frequency) sine and cosine waves present in the response rate data. Because we were interested only in how the total energy of the input signal was divided among the various frequencies, we present the results in terms of the magnitudes $|c_j|$, and focus our attention on the relative, not the absolute, values of these magnitudes. The latter was accomplished by dividing the magnitudes $|c_j|$ by their maximum value $|c_{\max}|$. A graph showing the energy at each frequency is called a power spectrum. Clear oscillatory behavior, such as the typical pause–peck cycles observed in a FI schedule, is revealed in the spectrum by higher energy at the frequency of $1/\text{FI}$. In contrast, a constant rate of responding yields the same energy at all frequencies.

2.2. Results and discussion

Fig. 1 shows samples of the cumulative records produced during the reinforcement and the extinction segments. To illustrate the range of results, we selected one pigeon from each group and then, for that pigeon, we selected the data from two sessions, the first session to show behavior immediately at the onset of extinction, and a subsequent session to show the best evidence, if any, of behavioral oscillations. Starting from the top, each set of two consecutive rows shows data from the first session (#1, first row), and from the fourth or fifth sessions (#4 or #5, second row) of Phase 2. In each row, the left panel shows the cumulative record for the last 10 reinforcement trials of the session, and the right panel shows the cumulative record for the subsequent extinction segment.

Consider the top two rows from pigeon P555 of group FI 16 s. The two left panels show the typical break-and-run patterns. The right panel from session 1 shows sustained pecking for the entire segment with a few pauses, decelerations, and accelerations around 160 s and 320 s. The right panel from session 5 shows a different pattern, namely, clear pause–peck cycles. By visual inspection, one can count 8 cycles during the first 160 s, and 16 cycles during the first 320 s. The next two rows, from pigeon P627 of group VI 16 s, show sustained pecking during the reinforcement trials and, with occasional variations in rate, also during the extinction segments. In contrast with the pigeon from the FI 16 s group, there were no main differences between the first and fifth sessions.

The data from the two other pigeons were similar. The left panels of pigeon P591 (FI 48 s group) show the typical break-and-run patterns. The first extinction segment shows sustained pecking for an interval greater than 10 times the FI parameter followed by some scallops between 600 s and 1200 s. Sustained pecking reappears at the end of the session. During the fourth session, pause–peck cycles started immediately after the onset of the extinction segment – by visual inspection we count 8 cycles during the first 480 s. The last two rows show the data of pigeon P179 (VI 48 s group). In the first session, sustained pecking occurred during both the reinforcement and extinction segments. In the fifth session, the pigeon pecked at a sustained and high rate for approximately 600 s and then alternated between a low and a high rate of pecking for the remainder of the session. No clear pause–peck cycles were observed.

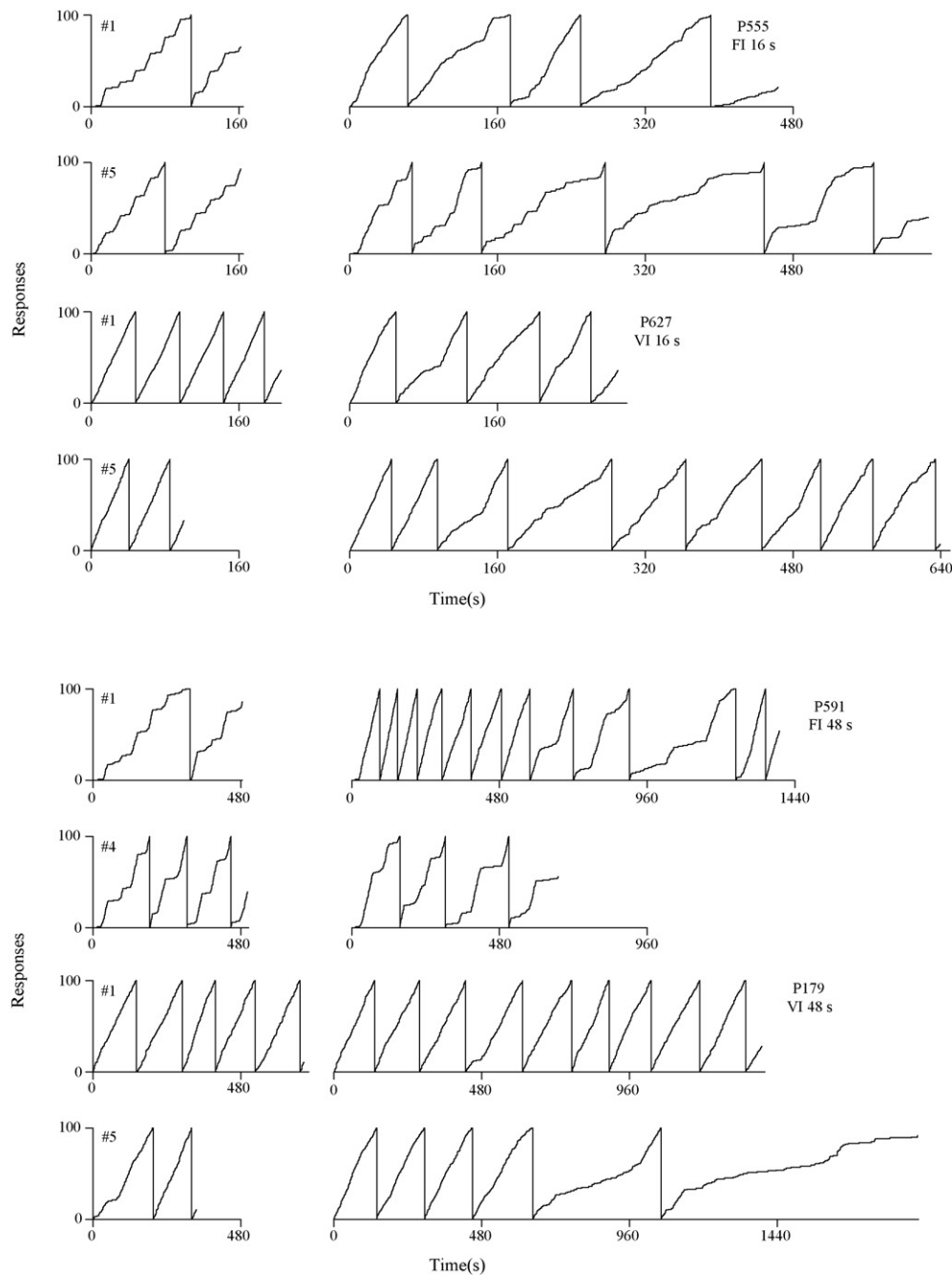


Fig. 1. Cumulative records from two sessions (the first and either the fourth or fifth) of one bird from each group. In each row, the left panel shows the last 10 reinforcement trials and the right panel shows the complete record of the extinction segment.

Fig. 2 shows the power spectra from the fourth or fifth sessions displayed in Fig. 1. Consider the top left panel, which is the spectrum for the last 10 reinforcement trials of the fifth session of P555 (FI 16 s). In this and all subsequent power spectra, both the ordinate and abscissa are linear scales. The length of each vertical line shows the “amount” of the corresponding frequency present in the overall signal. Given that food was received approximately every 16 s and the bird paused immediately after the food and started to peck roughly midway through the interval (cf. cumulative record in Fig. 1, second row, left panel), we expect most of the power to be near the frequency of $1/(16\text{ s})$, or 0.0625 Hertz (Hz), a value signaled in the figure by the triangle on the x-axis; all other frequencies should have low energy. This was indeed the case, as is evidenced by the

single spike at the predicted frequency. The same is true in the top right panel, which is the spectrum for the last 10 reinforcement trials of the fourth session of pigeon P591 (FI 48 s; cf. Fig. 1, six row, left panel). Most of the energy is concentrated in the frequency of 0.0208 Hz ($=1/48\text{ s}$).

The panels in the second row show the spectra for the first block in extinction. If, as the corresponding cumulative records in Fig. 1 suggest, the pause–peck patterns during extinction resemble the pause–peck patterns during reinforcement, possibly with slightly longer periods, then we would expect also high energy around the frequencies of 0.0625 Hz (left panel) and 0.0208 Hz (right panel) and around somewhat lower frequencies (i.e., at slightly longer periods). In other words, we would expect power spectra that

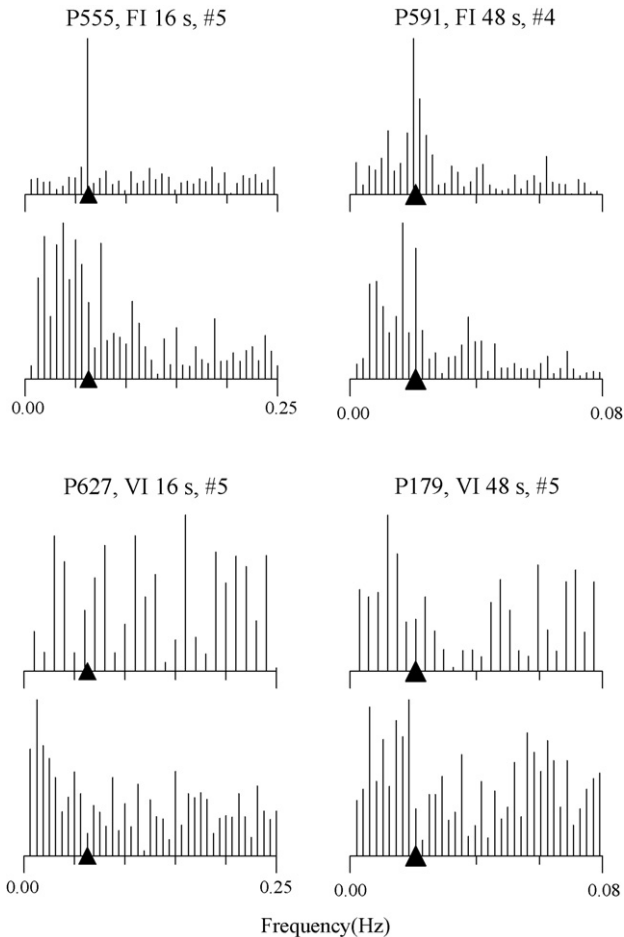


Fig. 2. Power spectra from session 4 or 5. For each subject, the top and bottom panels correspond to the last 10 reinforcement trials and the first extinction block, respectively. See Fig. 1 for the corresponding cumulative records. The triangle on the x-axis locates the reinforcement frequency, $1/(16\text{ s})$ or 0.0625 Hz for FI and VI 16 s groups and $1/(48\text{ s})$ or 0.0208 Hz for FI and VI 48 s groups. Both the abscissa and ordinate are linear scales.

looked like a generalization gradient, centered either at the reinforcement frequency or at a lower frequency. The two panels on the second row show that this was indeed the case. Most power was concentrated close to, but slightly to the left of, the reinforcement frequency. In the left panel, the highest spike was at 0.038 Hz (26.7 s); in the right panel the two highest spikes were at 0.017 Hz ($1/60\text{ s}$) and at the reinforcement frequency, 0.021 Hz ($1/48\text{ s}$). In both cases, little power was concentrated on higher frequencies.

The two bottom rows show the spectra for the VI birds. The energy was more evenly distributed over the frequency band, both during reinforcement and extinction. Compared to the FI spectra, the VI spectra showed less energy at the reinforcement frequencies and more energy at higher frequencies. The occasional high spikes in the VI spectra could not be related in any obvious way to the VI parameter. In fact, the VI spectra from these two birds, as well as from the other birds (not shown), resembled the “horizontal” spectrum expected from a Poisson process. That is, if responses occur at a constant rate with exponentially distributed inter-response times, the spectrum will show roughly the same energy across the frequency range.

The next two figures show the cumulative records and power spectra for the remaining pigeons of the FI groups; the data for the remaining pigeons of the VI groups were similar to those presented in the preceding figures and are not shown. Fig. 3 presents the best evidence of behavioral oscillations during the extinction segments for two other pigeons from the FI 16 s group (left panels) and the FI 48 s group (right panels). Pigeon P218 gave only 44 pecks during the first 55 s, but the power spectrum had the strongest concentration of energy (highest spike) at the frequency of $1/32\text{ Hz}$, the first harmonic of the reinforcement frequency. Pigeon P818 (session 6) produced a relatively long cycle followed by shorter cycles. By visual inspection, we count approximately 8 cycles at the end of 160 s. The power spectrum revealed high energy at the reinforcement frequency and slightly lower frequencies. Pigeon P380 also started extinction with a relatively long cycle followed by shorter cycles (visual inspection shows approximately 10 cycles in 480 s). The power spectrum revealed high energy at $1/60\text{ Hz}$, the highest spike, and neighboring frequencies.

Fig. 4 shows the cumulative records and the power spectra for pigeons P321 (FI 16 s group) and P819 (FI 48 s group). The abscissa for the power spectra are shown at the right. Unlike the other subjects from their groups, these pigeons revealed oscillations since the first session. Consider the data from P321. The cumulative record and the power spectrum on the left show, respectively, the break-and-run patterns during the reinforcement period and the spike at the reinforcement frequency. The cumulative record on the right panel shows a long run of pecking followed by clear pause–peck cycles. The power spectrum of the first 160-s block reveals higher energy at $1/23\text{ Hz}$ and $1/32\text{ Hz}$. The spectrum of the second 160-s block reveals higher energy at a larger band of frequencies (from $1/23\text{ Hz}$ to $1/13\text{ Hz}$) bracketing the reinforcement frequency. The DFT analysis was not performed on the third block because that block was shorter than 160 s. During the fifth session (rows 3 and

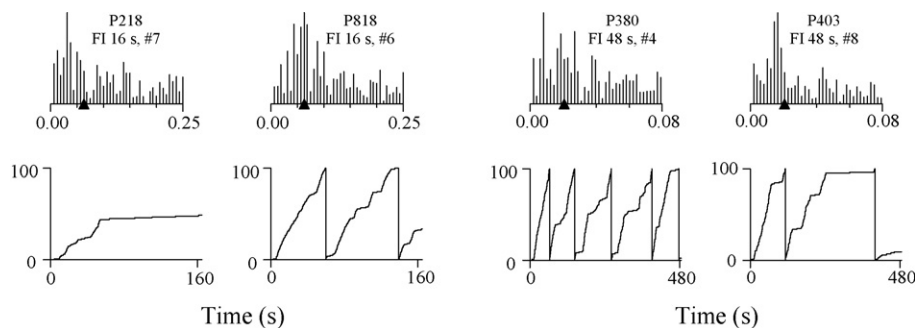


Fig. 3. For each bird, the two panels show the power spectrum (top) and cumulative record (bottom) from the first block of the extinction segment of one selected session. The triangle on the x-axis locates the reinforcement frequency, $0.0625\text{ Hz} = 1/(16\text{ s})$ for the FI 16 s pigeons and $0.0208\text{ Hz} = 1/(48\text{ s})$ for the FI 48 s pigeons.

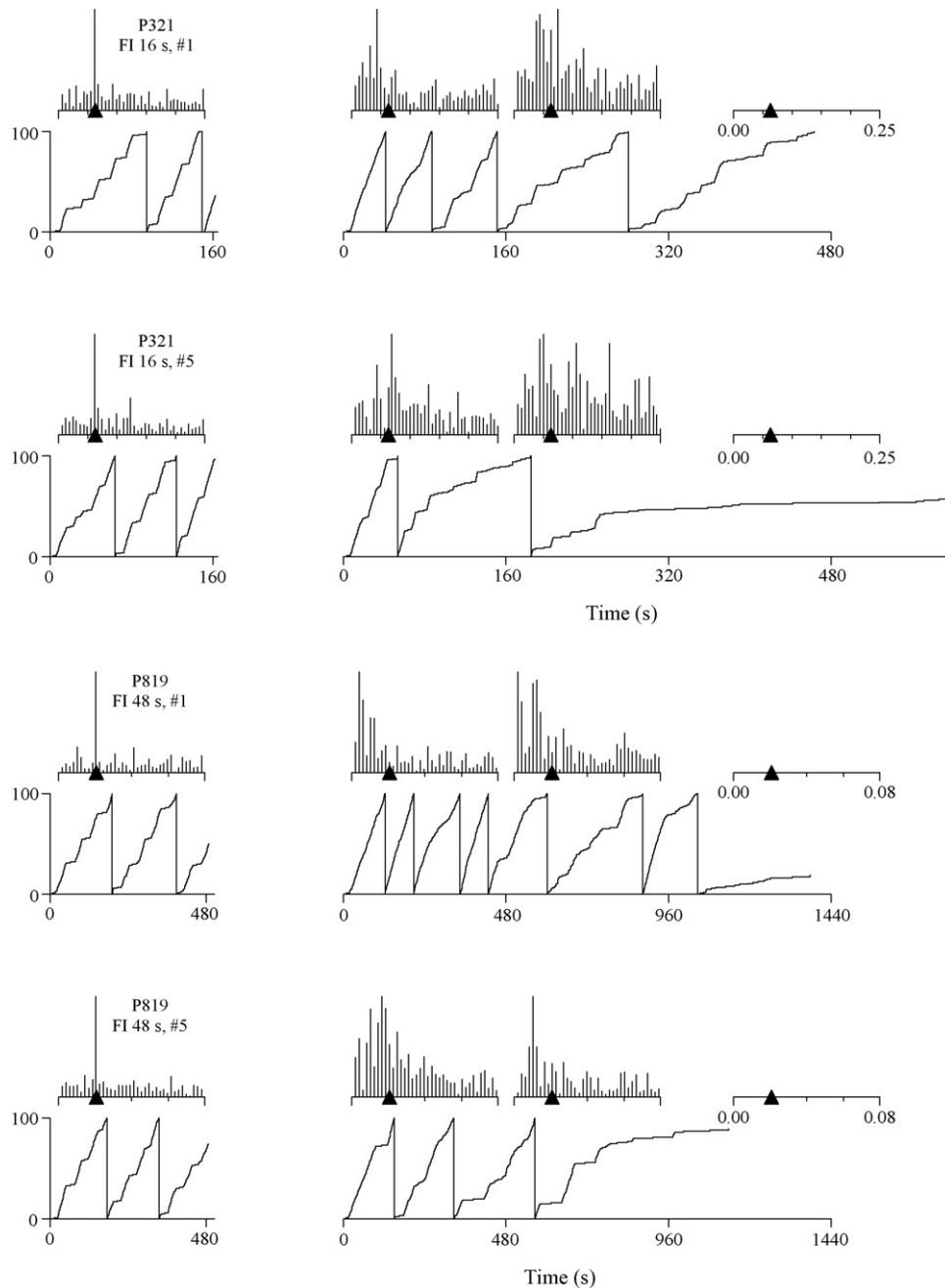


Fig. 4. Data from the first and fifth sessions of pigeons P321 and P819. The left panels show the power spectra and the cumulative records for the last 10 reinforcement trials. The right panels show the power spectra and the cumulative records for the extinction blocks. The frequency scale for the power spectra in each row is shown at the far right. The triangle on the x-axis locates the reinforcement frequency, $0.0625 \text{ Hz} = 1/(16 \text{ s})$ for the FI 16 s pigeon and $0.0208 \text{ Hz} = 1/(48 \text{ s})$ for the FI 48 s pigeon.

4), oscillations started immediately after the onset of extinction and the power spectra revealed high energy close to the reinforcement frequency (at $1/14.5 \text{ Hz}$ in the first block and at $1/20 \text{ Hz}$ in the second block).

The results from pigeon P819 were similar. In the first session, the clear break-and-run patterns observed during reinforcement (left panels) were followed, in extinction, by a long run for approximately 440 s, which in turn was followed by pause–peck cycles, although these cycles were not sharply defined. The power spectra revealed high energy at the lowest frequencies during the first 480-s block and at $1/60 \text{ Hz}$ and $1/96 \text{ Hz}$ during the second block. The bottom rows show the data from the fifth session. Oscillations started immediately in extinction and the power spectra revealed

high energy at the frequencies of $1/69 \text{ Hz}$ and $1/60 \text{ Hz}$ (first block) and $1/80 \text{ Hz}$ (second block).

To summarize the data regarding response rate oscillations in extinction, Fig. 5 displays average power spectra for the four groups. For the FI groups, the averages were computed from the individual spectra already displayed in Figs. 2–4. These spectra came from the first extinction block of the session with the clearest oscillations (across birds, sessions 4–8); they represent the best evidence for rate oscillations during extinction. For the VI groups, the averages were computed from the two individual spectra already displayed in Fig. 2 plus the spectra (not shown) from the remaining pigeons. To make the VI/FI comparison as meaningful as possible, we chose the VI spectra from a similar range of sessions (across birds, sessions

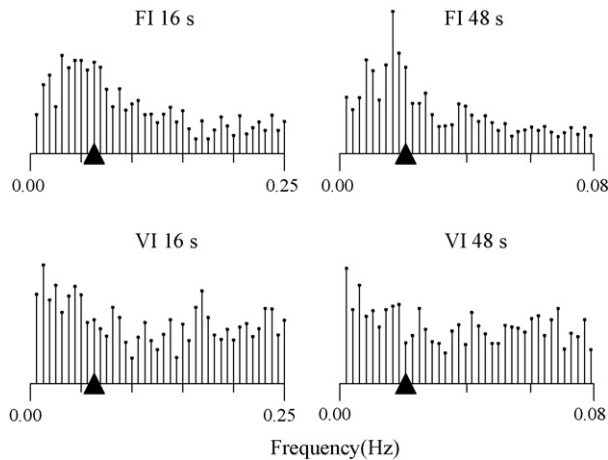


Fig. 5. Each panel shows the average power spectra for one of the four groups. The data for each pigeon came from the first extinction block of its “best” session (i.e., the session with the best evidence for oscillations). The triangles on the x-axes locate the reinforcement frequency, $0.0625 \text{ Hz} = 1/(16 \text{ s})$ for the 16-s groups and $0.0208 \text{ Hz} = 1/(48 \text{ s})$ for the 48-s groups.

2–8), restricted them to the first extinction block, and included the spectra that showed higher energy near the reinforcement frequency.

The average spectra confirm that the energy was dispersed more evenly through the various frequencies in the VI groups than the FI groups. Moreover, in the FI groups, relatively more energy was concentrated in the vicinity, but slightly to the left, of the reinforcement frequency.

The analysis of the cumulative records and the power spectra supported the following generalizations regarding behavior during the extinction segment. First, concerning the VI groups, the pigeons did not show regular pause–peck cycles. Response rate varied in the course of the extinction segment (e.g., Fig. 1, P179), but the variation rarely took the form of clearly defined pause–peck cycles. Response rate also varied across the extinction sessions – the pigeons tended to respond with lower rates and stop earlier, but there was substantial variability between subjects (e.g., some pigeons reduced responding notably after the second session but others only after the 12th session). Second, concerning the FI groups, in the first extinction session no pigeon showed pause–peck cycles immediately after the onset of the extinction segment although two birds, one from each group, showed some cycles at the end of the extinction segment. After 3–5 sessions, cycles were visible since the onset of the extinction segment, and the corresponding cumulative records showed consecutive break-and-run patterns with a length slightly longer than the FI parameter. The power spectra showed higher energy around the reinforcement frequency or at slightly lower frequencies. For both FI groups, after the 10th session response rate decreased, pauses became considerably longer, and the pause–peck oscillations became less reliable.

The preceding results corroborate and extend Machado and Cevik's (1998) findings according to which the response rate oscillations observed in extinction are related to the FI parameter. The two FI groups showed oscillations with different periodicities, 16 s or slightly longer in one case, 48 s or slightly longer in the other case. These oscillations did not occur when the average time between reinforcers remained the same, but strict periodicity was eliminated (VI groups). On the other hand, there was no evidence that the shorter FI yielded more or clearer oscillations than the longer FI.

3. Experiment 2: long extinction

In Experiment 1, as well as in Machado and Cevik's (1998) study, most pigeons from the FI groups showed more and clearer oscillations after a few sessions of Phase 2. This result suggests that periods of reconditioning and re-extinction may need to alternate at least a few times for pigeons to oscillate, perhaps because such alternation provides the opportunity for pigeons to learn the two ingredients necessary to oscillate, when to start pecking (learned during the FI trials), and when to stop pecking (learned during the extinction segment). On the other hand, two pigeons in Experiment 1 showed some pause–peck cycles at the end of the first session and this result, which Machado and Cevik (1998) also reported, suggests that oscillations may simply require sufficient time in extinction. One way to differentiate the two hypotheses is to increase considerably the length of the extinction segment of the first session. If more time in extinction suffices to generate oscillations in a larger number of pigeons, then the alternation of reinforcement and extinction would not be necessary. On the other hand, it is conceivable that alternations, although not necessary, may nevertheless increase the number of oscillations, sharpen them, or accelerate their onset. Experiment 2 tested these ideas.

The general procedure remained the same as in Experiment 1 except that when Phase 2 began the extinction segment lasted for a maximum of 3 h and 30 min. Thus, as in Crystal and Baramidze's (2006) study with rats, after extensive FI training, the animals were exposed to one very long extinction segment. The issues to be examined included (a) whether reliable oscillations would occur during the first session of extinction for a larger number of pigeons than in Experiment 1, (b) whether such oscillations would vary with the FI parameter, and (c) whether they would be absent in matching VI groups.

3.1. Materials and methods

3.1.1. Subjects

Twenty experimentally naive pigeons (*C. livia*) served as subjects. Housing conditions remained as in Experiment 1.

3.1.2. Apparatus

The equipment was the same as in Experiment 1.

3.1.3. Procedure

The pigeons were divided randomly into four groups of five subjects each: FI 16 s, VI 16 s, FI 48 s and VI 48 s. All details remained as in Experiment 1 except that in Phase 2 we increased the duration of the extinction segment to a maximum of 3 h and 30 min, or until the bird stopped responding for 30 consecutive minutes, whichever came first. Phase 2 lasted one session.

3.2. Results and discussion

Four of the FI 16 s pigeons responded almost continuously during the first 160-s block of the extinction segment. Bird P320 was the exception, as it displayed some pause–peck cycles after 80 s into the extinction segment. After the first block, some clear instances of oscillatory behavior were observed in three birds. The data from one of them, P319, are illustrated in the top row of Fig. 6. The left panel shows the last 10 reinforcement trials, with the typical break-and-run patterns, and the right panel shows the extinction segment. The pigeon responded at a high and sustained rate for slightly less than 160 s and then it started to pause and peck from 200 s to 360 s, reproducing the break-and-run patterns observed during the reinforcement period. By visual inspection, about 8 cycles can

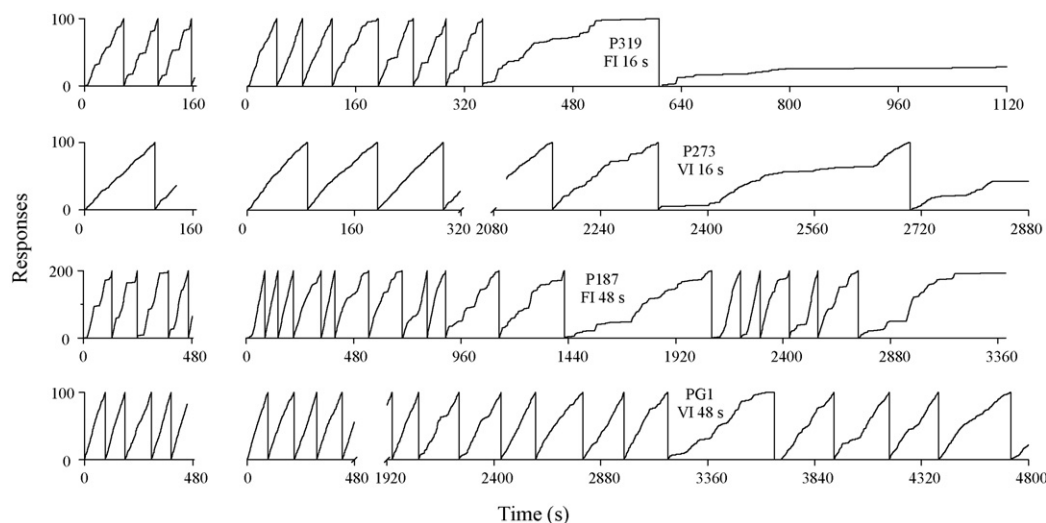


Fig. 6. A sample of cumulative records from Experiment 2. The curves on the left panels show performance during the last 10 reinforcement trials, and the curves on the right panels show the performance during the extinction segment.

be counted in that interval of time, which suggests that the oscillations were slightly longer than the FI parameter. Thereafter the oscillations disappeared, and after 500 s the pigeon responded only occasionally. The remaining pigeons from group FI 16 s showed similar behavior, although the pause–peck cycles were not as sharply defined as they were in Experiment 1. The cumulative record of one pigeon, P770, did not show any reliable cycles.

The VI 16 s pigeons responded at a constant and moderate rate for a long period of time. The second row of Fig. 6 shows one example. Response rate during the first part of the extinction segment was similar to the response rate during the reinforcement trials. It changed appreciably only after 2100 s, but clear pause–peck cycles similar to break-and-run patterns or scallops were never observed.

Concerning the FI 48 s group, all pigeons responded at a steady rate for at least the first 480-s block. Then, pausing and pecking started to alternate, somewhat irregularly. Reliable pause–peck cycles were observed during some intervals of time, but they tend to be short-lived and not as sharply defined as in Experiment 1. The third row of Fig. 6 shows one example. During the reinforcement trials, scallops and break-and-run patterns are clearly visible. During the extinction segment, pecking starts to alternate with pausing after approximately 480 s, but clear pause–peck cycles occurred only briefly between 900 s and 1200 s and between 2400 s and 2900 s.

The VI 48 s pigeons responded throughout the extinction segment. Response rate changed during extinction but pause–peck cycles were observed rarely. The bottom row of Fig. 6 shows the data of one pigeon from this group. The sustained rate of pecking, observed during the reinforcement trials, was maintained during a long period in extinction. After 2000 s approximately, occasional pauses were observed and between 3000 s and 3500 s some cycling takes place, although the cycles are not sharply defined. For a more quantitative analysis of behavioral oscillations, we turn to the DFT analysis.

The next four figures show the power spectra for the four groups. In each figure, each row shows the data from the first three blocks of the extinction segment of one pigeon; the bottom row shows the group averages. Consider Fig. 7, from the FI 16 s group. In the left panels the energy is either dispersed across a broad band of frequencies (e.g., P319 and P9034) or concentrated at the lowest frequencies (e.g., P320 and P770). The former spec-

tra correspond to constant rates of pecking throughout the block; the latter spectra correspond to variations in rate, typically decelerations, from the beginning to the end of the block. In any case, these spectra do not correspond to reliable oscillations. In contrast, the middle panels reveal in at least three cases (P319, P320, and P9034; see also the average spectrum) a more uneven distribution of energy, with greater concentrations at frequencies close to, but slightly lower than, the reinforcement frequency. These spectra are consistent with pause–peck oscillations. However, as the right panels reveal, these oscillations were short-lived, as in most cases the energy concentrated again on the lowest frequencies.

Fig. 8 shows the spectra for the FI 48 s group. For three pigeons, oscillatory-like spectra were evident during the second block (P502, P685, and PG9), in all cases with maximum energy at frequencies less than the reinforcement frequency (1/68 Hz for PG9, 1/120 Hz for P502 and P685; see also the average spectrum). For one pigeon, P187, oscillations were evident during the third block, with maximum energy concentrated at the reinforcement frequency. For pigeon PG3, the third block also showed a slow rate oscillation with period 240 s.

Figs. 9 and 10 show the spectra for the VI 16 s and the VI 48 s groups, respectively. In both cases, the energy was generally distributed over the entire frequency range, as is expected when response rate is roughly constant. Occasionally, though, the energy was concentrated at one of the lowest frequencies (e.g., Fig. 10, P639 and PG1) because response rate varied slowly during the block. One spectrum in Fig. 9 (see PG2, left panel) is probably an artifact because the pigeon paused for approximately 120 s after emitting only 38 responses in 25 s. Most likely, this pause was caused by an extraneous sound.

Finally, to compare the DFT data from Experiments 1 and 2, Fig. 11 re-plots the average spectrum from each group from the two experiments. The spectra from Experiment 2 came from the second block of extinction, because most oscillations occurred during that block; the spectra from Experiment 1 are the same as in Fig. 5. For the FI groups, the average spectra have the same general shape, with more energy at frequencies slightly less than the reinforcement frequency and less energy both at higher frequencies and at the lowest frequencies sampled. However, in the FI 16 s groups, the spectrum from Experiment 2 has notably more energy at higher frequencies, which is consistent with the idea that in Experiment 2 the

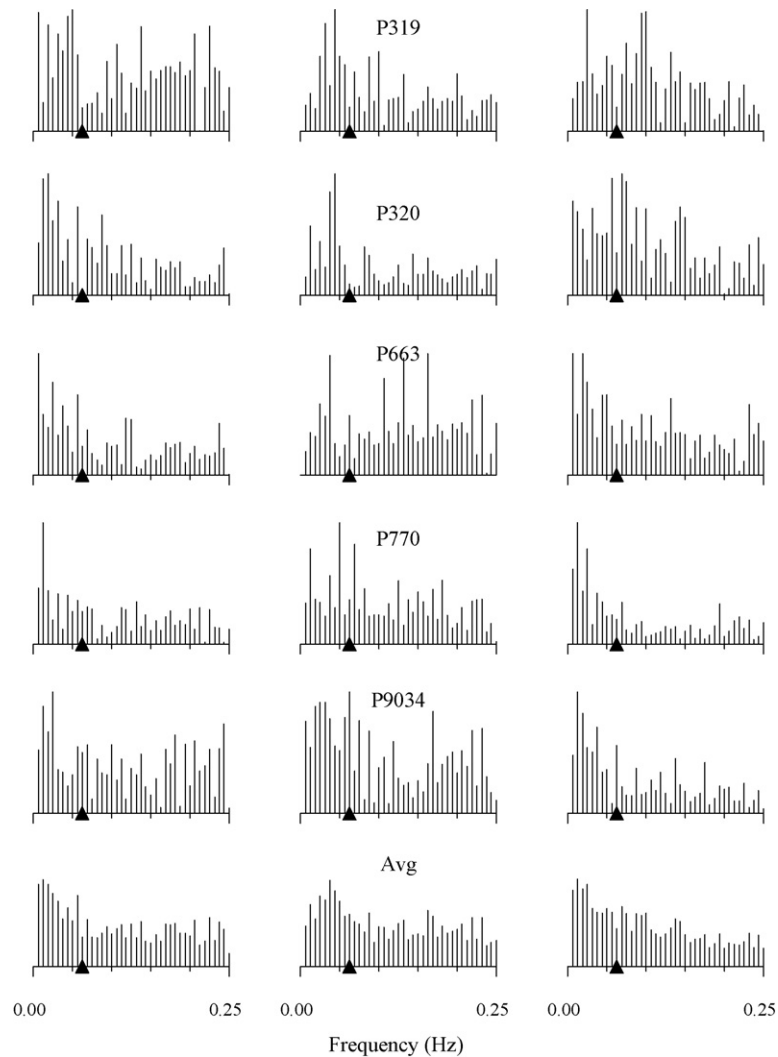


Fig. 7. Power spectra for all birds of the FI 16 s group. Each row shows the data from the first three blocks of the extinction segment (each block corresponds to 160 s). The bottom row shows the group average per block. The triangles on the x-axes locate the reinforcement frequency (0.0625 Hz).

oscillations were not as clearly or sharply defined as in Experiment 1. In the FI 48 s groups, the spectrum from Experiment 2 has energy less concentrated around the reinforcement frequency than the spectrum from Experiment 1. The narrower spectrum from Experiment 1 is also consistent with the idea that oscillations were more sharply defined in that experiment.

The average spectra from the VI groups, whether 16 s or 48 s, had similar shapes. The energy was spread over the entire frequency range, either evenly (Experiment 2) or with slightly greater concentrations at the lowest frequencies (Experiment 1). The latter finding was due in general to slow decelerations typical of extinction curves.

To summarize, the results from Experiment 2 partly replicate with pigeons the results reported by [Crystal and Baramidze \(2006\)](#) with rats. Like rats, pigeons also show response rate oscillations during extinction after FI training but, unlike rats, pigeons do not show oscillations immediately after the onset of extinction. When compared with the results from Experiment 1, the results from Experiment 2 also suggest that (a) lengthening the first extinction segment increases the number of pigeons that show oscillations. However, (b) these initial oscillations are not as reliable or as sharply defined as when periods of reinforcement alternate with periods of extinction. In addition, (c) the absence of reliable

oscillations in the VI groups in both experiments shows that reinforcement periodicity is necessary for oscillations to occur. And finally, (d) a few pigeons simply do not oscillate, at least in a way clearly related to the FI parameter.

4. Experiment 3: extinction following the peak procedure

Our results suggest that experience with reconditioning and re-extinction may be necessary to obtain two effects, well-defined oscillations with a period clearly related to the FI parameter, and the rapid onset of these oscillations once extinction begins. The reason for these effects may be that the alternation of reconditioning and re-extinction segments gives the pigeons the opportunity to learn to start responding near the time of food availability (during food trials), and to stop responding once that time has elapsed (during non-food trials).

If this interpretation is correct, then we predict that training pigeons in a peak procedure, with food trials (as in FI schedules) interspersed with non-food trials (as in extinction), and exposing them next to an extinction segment should generate well-defined oscillations, with a period clearly related to the FI parameter. In addition, these oscillations should occur immediately once extinction starts. Experiment 3 tested these ideas.

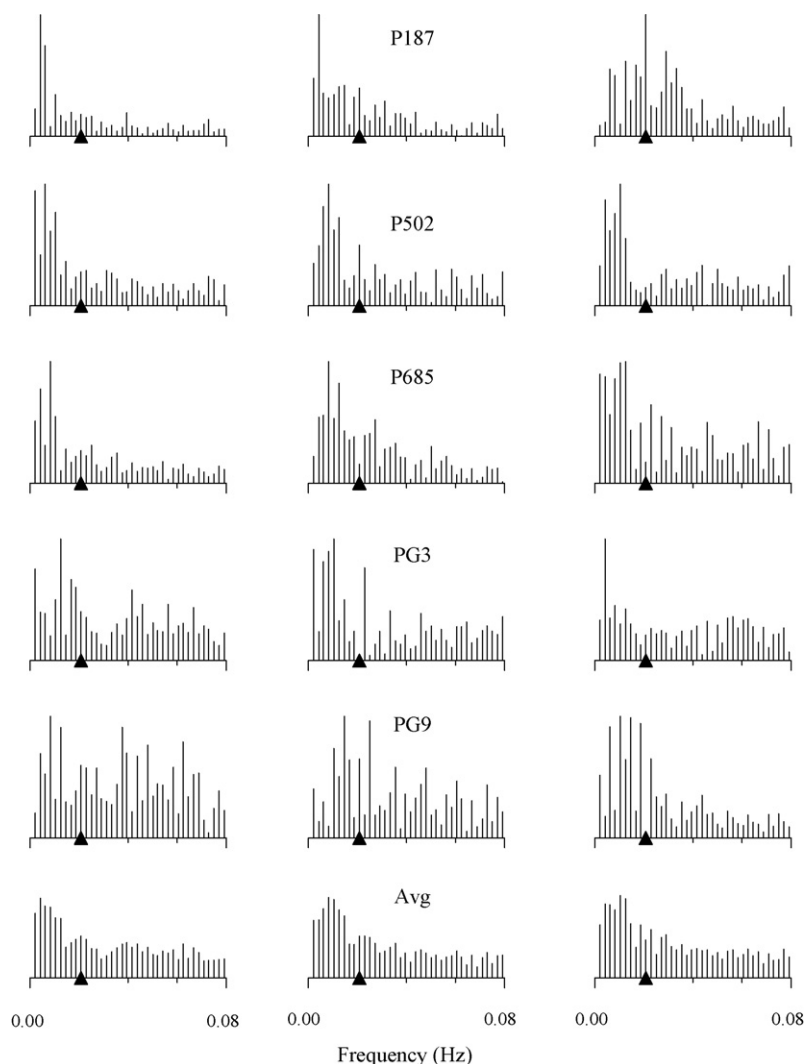


Fig. 8. Power spectra for all birds of the FI 48 s group. Each row shows the data from the first three blocks of the extinction segment (each block corresponds to 480 s). The bottom row shows the group average per block. The triangles on the x-axes locate the reinforcement frequency (0.0208 Hz).

4.1. Methods and materials

4.1.1. Subjects

Ten naive pigeons (*C. livia*) participated in the experiment. The treatment of the subjects was as in Experiments 1 and 2.

4.1.2. Apparatus

The equipment was the same as in Experiments 1 and 2.

4.1.3. Procedure

All pigeons learned to peck the key through the autoshaping method (4–5 sessions). Then they were assigned randomly to one of two groups and each group went through the three phases of the experiment.

4.1.3.1. Phase 1: FI training. During this phase, one group was trained on a FI 20-s schedule and the other on a FI 40-s schedule. At the beginning of each trial, the houselight was turned on and the central key was illuminated with red light. The first peck after the fixed interval elapsed turned off the key and houselights and raised the food hopper from 3 s to 5 s. During the first sessions, the hopper duration was adjusted for each bird to minimize extra-session

feeding. A 10 s (FI 20 s group) or 20 s (FI 40 s group) ITI, beginning at the offset of the hopper, separated the trials. Sessions ended after 40 trials and lasted 30 days.

4.1.3.2. Phase 2: peak interval training. In addition to FI trials, each session contained also non-food, peak interval trials that were four times longer than the FI trials. Every session started with 10 FI trials which were followed by 10 blocks of 4 trials each, for a total of 50 trials. Each block contained three FI trials and one PI trial in random order. This phase lasted 60 sessions.

4.1.3.3. Phase 3: extinction. Each session started as before, with 10 FI trials followed by a variable number (between 3 and 7) of blocks of 3FI–1PI trials, which in turn were followed by a relatively long extinction segment. The variable number of blocks meant that extinction began unpredictably within a session. During the extinction segment the houselight and the keylight remained illuminated, as in the regular FI and PI trials. The extinction segment lasted for the remainder of the session, that is, until an interval equivalent to the 50 trials of Phase 2 had elapsed. Thus the sessions had approximately the same duration in Phases 2 and 3. This phase lasted six sessions.

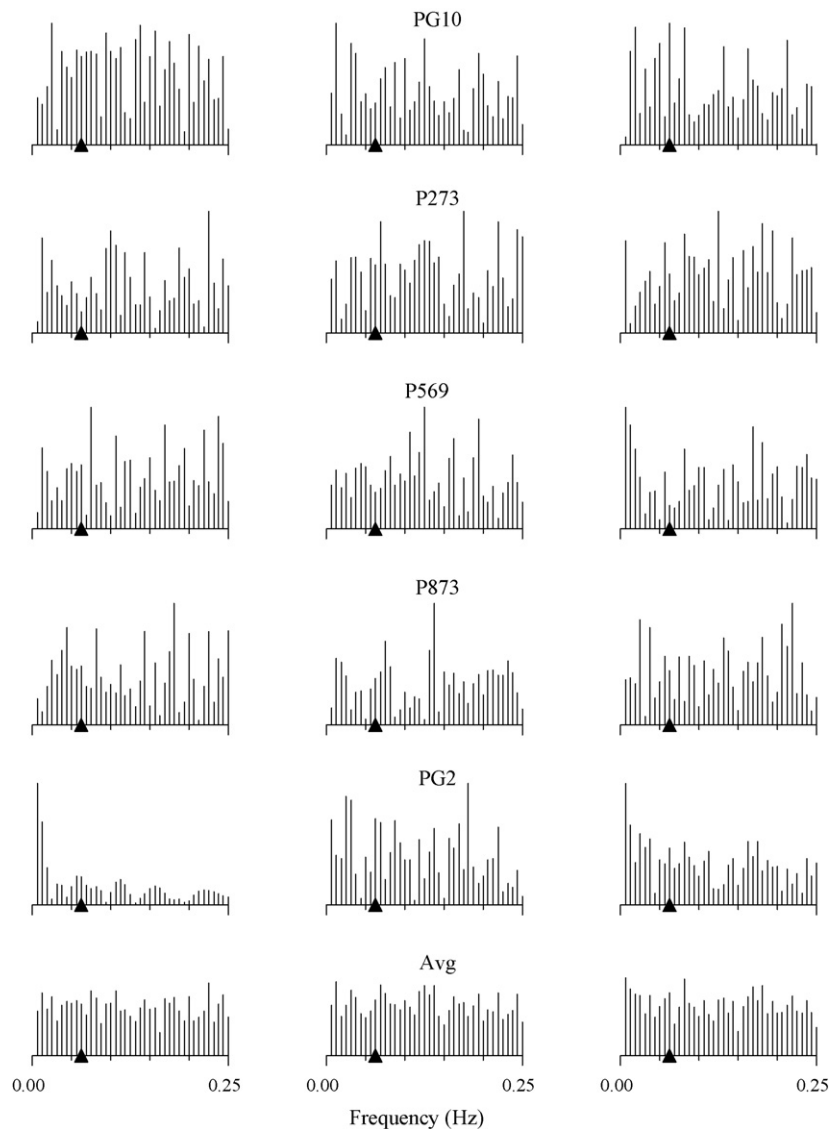


Fig. 9. Power spectra for all birds of the VI 16 s group. Each row shows the data from the first three blocks of the extinction segment (each block corresponds to 160 s). The bottom row shows the group average per block. The triangles on the x-axes locate the reinforcement frequency (0.0625 Hz).

4.1.4. Data analysis

The input to the DFT analysis consisted of the number of responses produced during consecutive 2 s bins (FI 20 s PI 80 s group) or 4 s bins (FI 40 s PI 160 s group), for a total of 120 bins. Thus, the input samples were always 240-s long for the FI 20 s PI 80 s group, and 480-s long for the FI 40 s PI 160 s group, in both cases the duration of three PI trials. As in Experiments 1 and 2, the data were linearly detrended before the DFT analysis and no windowing was used.

4.2. Results and discussion

When the PI trials were first introduced in Phase 2, the majority of birds in both groups responded continuously after the time when food was primed on food trials. This pattern of sustained pecking was observed for the first 4 days. From the 5th day onwards, the birds started to pause after twice the length of the regular FI trial (i.e., at $t = 2\text{FI}$ s). This means that, on PI trials, pigeons in the FI 20 s PI 80 s group started to respond roughly at 10 s, reached a maximum response rate around 20 s, then reduced responding and tended to

pause around 40 s (2FI). The pigeons in the FI 40 s PI 160 s group behaved similarly: They started to respond around 20 s into the trial, reached a maximum response rate around 40 s and paused at approximately 80 s (2FI). These pause–peck–pause cycles had a period twice the length of a regular FI trial.

Around the fifth session of Phase 2, 7 of the 10 pigeons (2 from group FI 40 s PI 160 s and all 5 from group FI 20 s PI 80 s) presented a second response rate peak centered at approximately $t = 3\text{FI}$. These results replicate Kirkpatrick-Steger et al.'s (1996) results concerning double peaks in the peak procedure. However, as in Sanabria and Killeen's (2007) study, during the last four sessions of training 7 of the 10 pigeons did not show a second peak but a ramp (i.e., average response rate increased monotonically from $t = 2\text{FI}$ until the end of the trial). Hence, our results from Phase 2 partly replicate each of these studies. We will return to these findings in Section 5.

Concerning the extinction phase, a preliminary analysis of the cumulative records revealed that the first session of Phase 3 contained the clearest instances of oscillatory performance for all pigeons of the FI 20 s PI 80 s group, and for all but one pigeon of

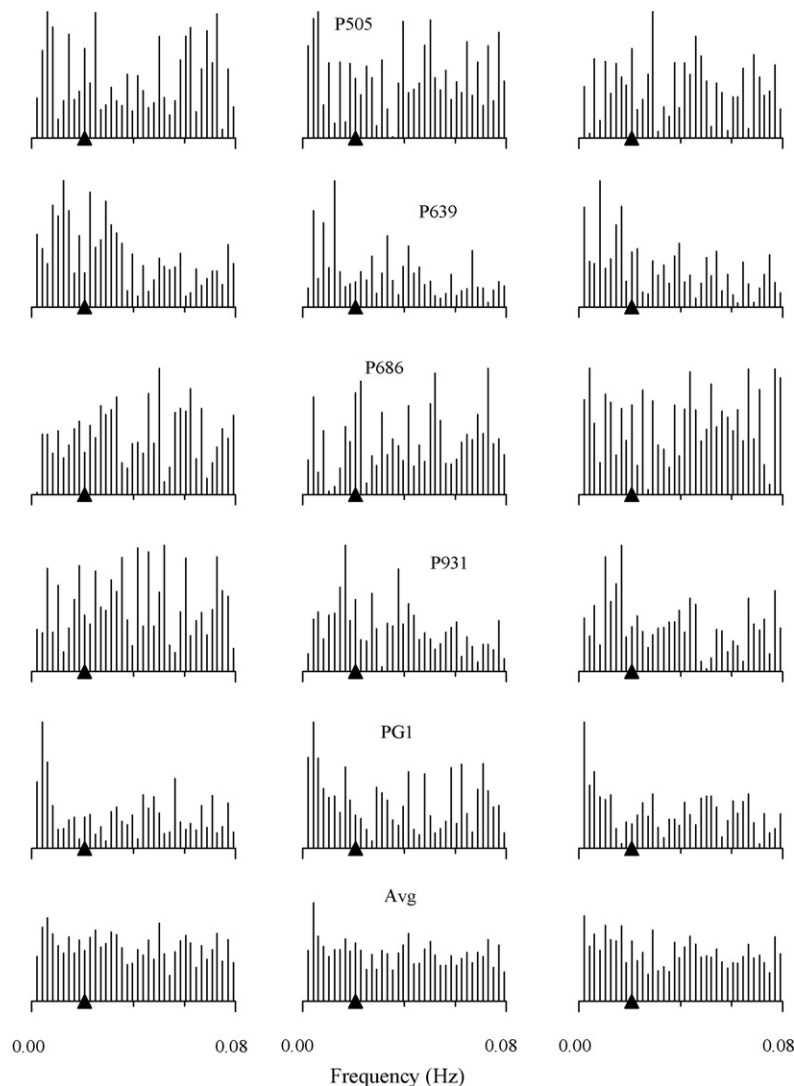


Fig. 10. Power spectra for all birds of the VI 48 s group. Each row shows the data from the first three blocks of the extinction segment (each block corresponds to 480 s). The bottom row shows the group average per block. The triangles on the x-axes locate the reinforcement frequency (0.0208 Hz).

the FI 40 s PI 160 s group. For this reason, the analysis of response rate oscillations was restricted to the first session.

Fig. 12 shows the cumulative records and the power spectra for the five pigeons of group FI 20 s PI 80 s. The left panels show the records and spectra for the last three PI trials that preceded the extinction segment; the right panels show the records and spectra for the extinction segment. The three PI trials on the left panels are presented as if they were consecutive trials in order to define a sort of baseline against which behavior in extinction could be compared. Above each 240-s block of the cumulative record is the corresponding power spectrum for that block. The frequency scale for all power spectra is shown at the far right of the first and last rows.

For three birds (P197, P013, and P188), the cumulative records of the PI trials showed the distinctive scallops or break-and-run patterns. A close inspection of each PI trial reveals that two pigeons, P197 and P188, generally paused, pecked, paused, and then pecked again, occasionally making a third pause just before the trial ended. Pigeon P013 did not pause distinctively after the time of food, but it reduced its rate of responding considerably yielding two distinct slopes in the cumulative record. Pigeon P284 started to respond immediately at trial onset and then, after the time of food, either

it paused, pecked briefly, and then responded at a much lower rate till the end of the trial, or it responded at a lower rate till the end of the trial. In contrast with the preceding results, P190 showed only small variations in response rate during the PI trials.

What should the power spectra in the peak procedure look like? If, as some cumulative records suggest, from $t=0$ s to $t=2$ FI s a pigeon pauses, pecks, and then pauses again, and then from $t=2$ FI s to $t=4$ FI s the pigeon repeats this pause–peck–pause performance, then the spectrum will yield the greatest amount of energy at the $1/2$ FI frequency, where the triangles are in the figure. However, if a pigeon pauses and pecks and then does not repeat the pause–peck cycle but either pauses or responds at a low but increasing rate till the end of the trial (ramp), then the spectrum will yield the greatest amount of energy at the $1/4$ FI frequency because, in this case, the repeating unit is the entire PI trial performance which lasts 4FI s, the duration of the PI trial. Obviously, a mixture of these two behavioral patterns is possible, in which case energy will be concentrated at the two frequencies, $1/2$ FI and $1/4$ FI.

The power spectra of Fig. 12 (left panels) show all these cases. The spectra of P197 and P188 show spikes mainly at half the reinforcement frequency ($1/2$ FI; see triangles on the x-axis); the spectrum for P190 show energy mainly at the $1/4$ FI frequency; and

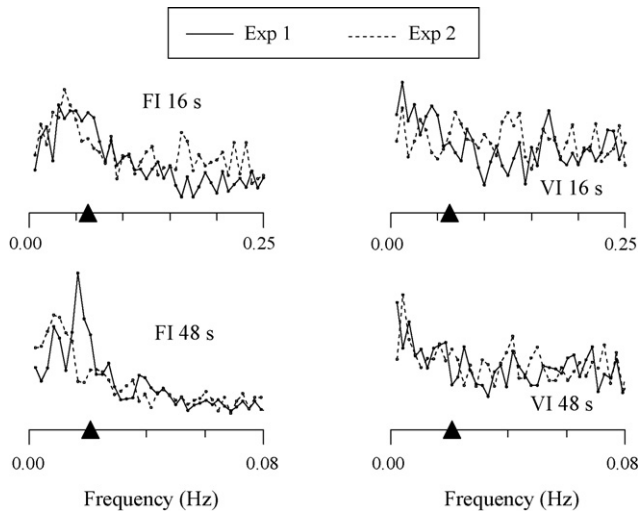


Fig. 11. Average spectrum from each group in Experiments 1 and 2. The spectra from Experiment 2 (broken lines) came from the second extinction block. The spectra from Experiment 1 (solid lines) are the same as in Fig. 5. The triangles on the x-axes locate the reinforcement frequency, 0.0625 Hz = $1/(16\text{ s})$ for the FI and VI 16 s groups and 0.0208 Hz = $1/(48\text{ s})$ for the FI and VI 48 s groups.

the spectra from pigeons P013 and P284 show spikes at the two frequencies of $1/2\text{FI}$ and $1/4\text{FI}$.

During the extinction segment, all pigeons showed pause–peck cycles. These cycles began immediately and, for most pigeons, continued until the end of the session. They were particularly well defined for the four pigeons (except P190) that had shown good rate differentiation during the PI trials. In some cases, the clarity and sharpness of the cycles improved across the first blocks in extinction (e.g., P197: cf. blocks 2 and 3; P013: cf. first 3 blocks; P188: cf. block 4). Again, the exception was pigeon P190, for though pause–peck cycles occurred (cf. block 4), they were not clearly defined. Most behavior oscillations in extinction had periods close to 2FI .

Fig. 13 shows the data for the FI 40 s PI 160 s group. The cumulative records on the left panels reveal a variety of patterns during the PI trials: two pause–peck–pause cycles (e.g., P100 and P343), similar cycles without the final pause (e.g., P184), peck–pause–peck–pause cycles (e.g., P334), or peck–pause–peck cycles (cf., P184). The power spectra reveal high energy at the $1/2\text{FI}$ or nearby frequencies.

The data on the right panels show that response rate oscillations occurred since the onset of the extinction segment and were maintained for long intervals of time. The oscillations were remarkably clear in some blocks (e.g., P100, blocks 1–3; P132, block 2; P184, block 2; P334, blocks 1–3; P343, blocks 1 and 2). Most energy was concentrated at the frequency of $1/2\text{FI}$ or nearby frequencies (cf. the frequency scale for all power spectra at the far right of the first and last rows).

To summarize the data, Fig. 14 shows the average spectra during the last three PI trials and the first three blocks in extinction. These averages were calculated from the individual spectra shown in Figs. 12 and 13. For example, the average curve for the PI trials of group FI 20 s PI 80 s (top left panel of Fig. 14) was calculated from the first spectrum in each row of Fig. 12. Similarly, the average curve for the first extinction block of group FI 40 s PI 160 s (filled circles in the bottom right panel of Fig. 14) was calculated from the second spectrum in each row of Fig. 13. The top curves in Fig. 14 show that, during the PI trials, the energy was unevenly distributed, with low energy at the highest frequencies and high energy at $1/2\text{FI}$ and $1/4\text{FI}$ (duration of PI trial) frequencies. The average spectra during extinc-

tion were similar, with little energy at the higher frequencies and most energy concentrated close to $1/2\text{FI}$. There were no systematic differences in the spectra for the three extinction blocks.

Fig. 15 compares the average data of the FI groups from the three experiments. (Note that the number of FI training trials was similar across experiments and legitimizes the comparison – between 3000 and 3500 FI trials in Experiments 1 and 2, and 3600 FI trials in Experiment 3.) To make the different FI groups directly comparable, all frequencies were divided by the reinforcement frequency of the group (in Experiments 1 and 2: $1/16$ for FI 16 and $1/48$ for FI 48 groups; in Experiment 3, $1/20$ for FI 20 PI 80 and $1/40$ for FI 40 PI 160). Furthermore, a four-parameter Gaussian function was fitted to each data set in order to estimate the frequency with the highest energy. The function had equation $y(f) = a + b \exp(-0.5 \times (f - \mu)^2 / \sigma^2)$, where f stands for relative frequency, and a , b , μ , and σ are free parameters. The function reaches its maximum value when $f = \mu$. In Experiment 1, the best-fitting μ equaled 0.79 (FI 16) and 0.75 (FI 48); in Experiment 2 it equaled 0.60 (FI 16) and 0.42 (FI 48) and in Experiment 3 it equaled 0.40 (FI 20 PI 80) and 0.46 (FI 40 PI 160). That is, the estimated relative frequency with maximum energy was located in the interval 0.4–0.8, which corresponds to periods of 2.5–1.25 times the FI parameter. The data and the fitted functions also suggest that oscillations were most regular in Experiment 3, and least regular in Experiment 2 (irregularity is indicated by variability and high energy at the highest frequencies). Finally, the data and curves from the two FI values in each experiment are reasonably close, particularly in Experiments 1 and 3, a result that suggests superposition of the behavioral oscillations, as Machado and Cevik (1998) reported.

5. General discussion

While a playground swing is being pushed it oscillates with a particular frequency. When the pushing stops, the swing continues to oscillate with approximately the same frequency but with lower amplitude until it stops. FI schedules may be conceived analogously, with food delivery and other time markers being the equivalent of the pushing and the pause–peck cycles, break-and-run patterns, or FI scallops being the equivalent of the oscillations. The issue then is whether behavior will continue to oscillate when reinforcement ceases. To distinguish oscillations forced externally by the reinforcer from oscillations observed in the absence of the reinforcers and under constant environmental conditions, we call the latter “spontaneous oscillations”. Under what conditions will spontaneous oscillations occur? What determines their period and how is their period related to the period of the forced oscillations? What processes underlie spontaneous oscillations? How are these processes related to processes assumed by current theories of timing? These are some of broad questions raised in the study of behavioral oscillations.

The present study attempted to characterize the behavior of pigeons in extinction after exposure to periodic reinforcement. We suggested that this general goal could be reached through different methodologies. In Experiment 1 we exposed pigeons to extensive FI training and then to daily segments of reconditioning and re-extinction. The study replicated Machado and Cevik's (1998) original study and extended it by incorporating adequate VI control groups. Our findings showed that during the first extinction segment, the pigeons responded uninterruptedly for intervals much longer than the FI parameter. Although a few birds showed pause–peck cycles later in the extinction segment, the majority of birds required 3–5 sessions of reconditioning and re-extinction to show spontaneous oscillations reliably since the onset of the extinction segment. After approximately 10 sessions, the pigeons made substantially longer pauses in

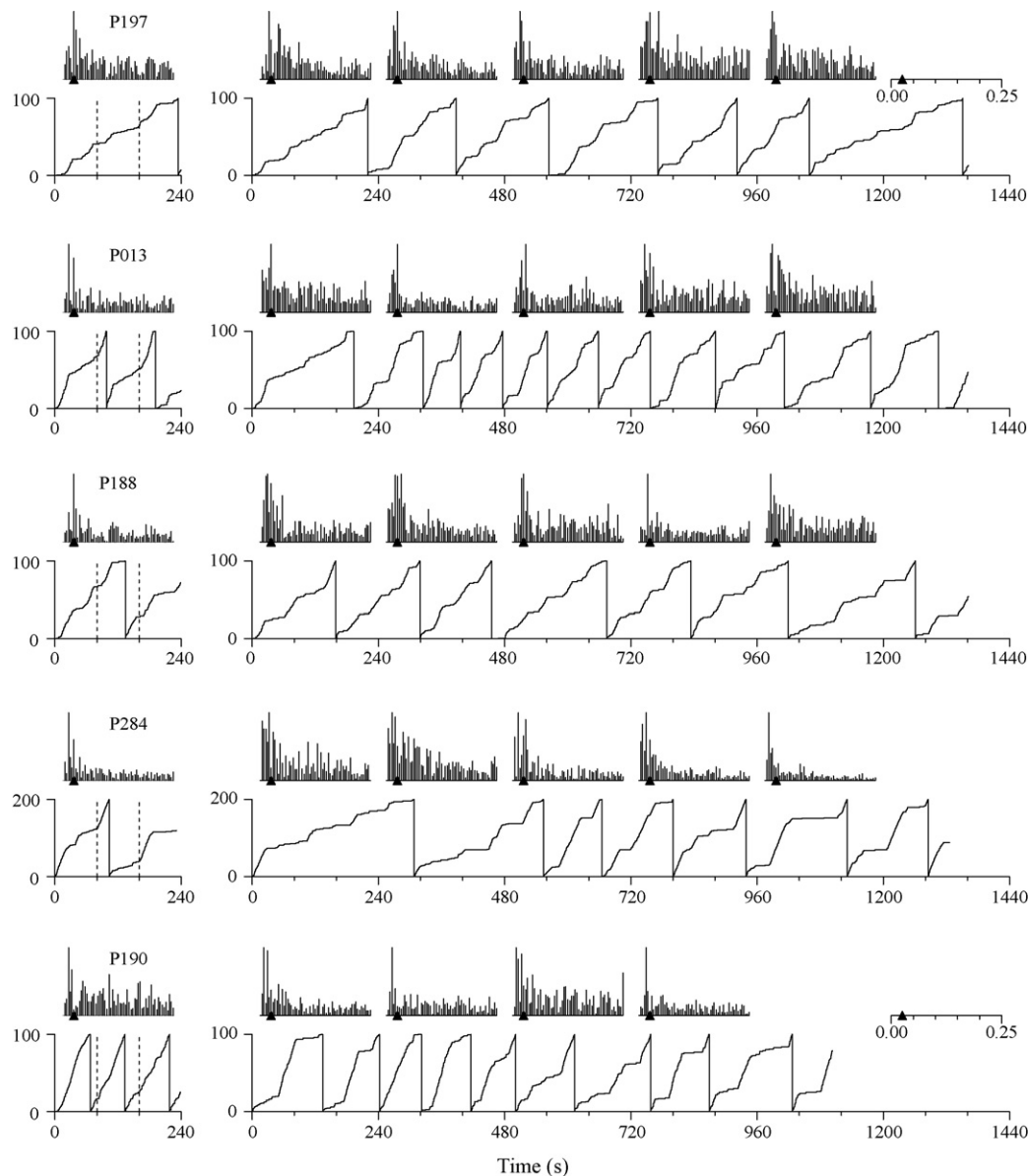


Fig. 12. Cumulative records and power spectra for the five pigeons of group FI 20 s PI 80 s. The left panels show the records and spectra for the last three PI trials that preceded the extinction segment; the right panels show the records and spectra for the extinction segment. Above each 240-s block of the cumulative record is the corresponding power spectrum. The frequency scale for the power spectra is shown at the far right of the first and last rows. The triangles on the x-axes locate the frequency of $1/(2FI) = 0.025$ Hz.

the absence of food or ceased to respond early in the extinction segment. In contrast, the pigeons exposed to matching VI schedules responded continuously throughout the first extinction segment. In fact, sustained pecking was observed on most extinction segments, although the pigeons showed decelerations within segments and also ceased to respond earlier in subsequent sessions.

The spontaneous oscillations revealed in the cumulative records of the FI groups were found by a discrete Fourier transform analysis to have periods close to or slightly longer than the FI values. The power spectra of these groups had highly asymmetric distributions of energy, with little energy at the high frequencies and more energy at the reinforcement frequency ($1/FI$) and shorter frequencies. In contrast, the power spectra from the VI groups had energy distributed over all frequencies, in particular, the high frequencies. The spectra for the VI groups were similar to the theoretical horizontal spectrum engendered by a Poisson process (i.e., constant

rate of responding with exponentially distributed inter-response times).

These findings, as well as those reported by Machado and Cevik (1998), are consistent with the summary observation made by Ferster and Skinner (1957) regarding extinction following FI training: "The most obvious interpretation is that the interval performance follows whenever the bird has been pausing for any length of time." (p. 197). They add precision to this broad statement because they show that, once food is removed, the pigeons take a large amount of time (relative to the FI value) to start pausing; the interval performance follows, as Ferster and Skinner stated, but typically with a period longer than the FI; the oscillatory performance depends on the periodicity of food because similar average interfood intervals without periodicity (VI groups) do not engender the same performance.

Experiment 1 and Machado and Cevik's (1998) study showed that a minority of pigeons oscillate late in the first extinction seg-

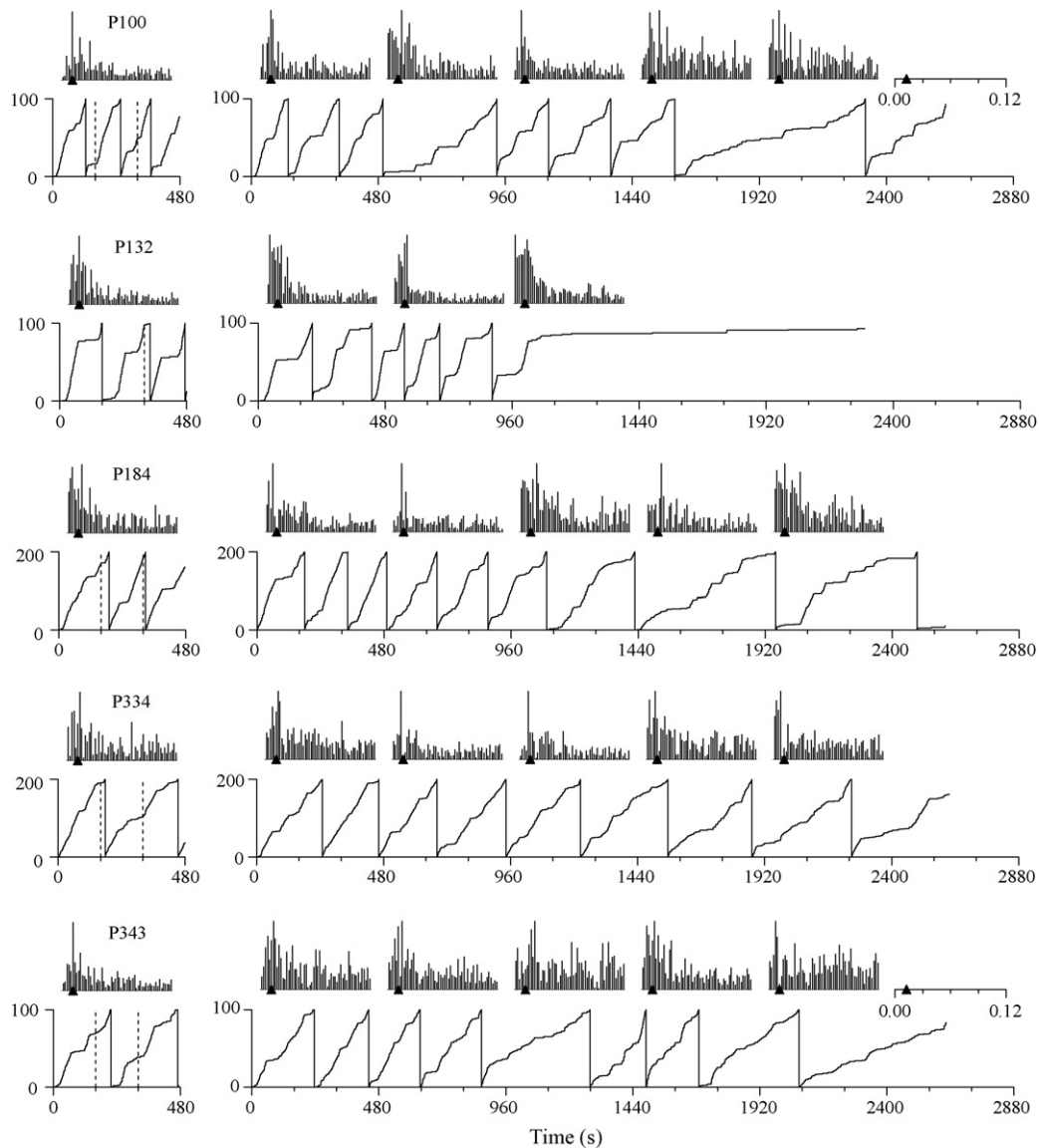


Fig. 13. Cumulative records and power spectra for the five pigeons of group FI 40 s PI 160 s. The left panels show the records and spectra for the last three PI trials that preceded the extinction segment; the right panels show the records and spectra for the extinction segment. Above each 480-s block of the cumulative record is the corresponding power spectrum. The frequency scale for the power spectra is shown at the far right of the first and last rows. The triangles on the x-axes locate the frequency of $1/(2FI) = 0.0125$ Hz.

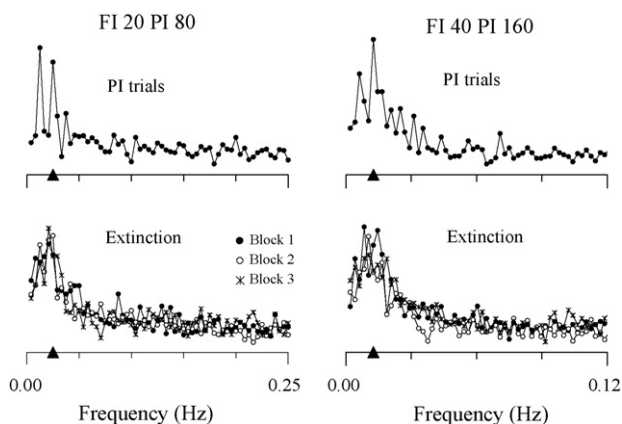


Fig. 14. Average spectra for each group during the last three PI trials and the first three extinction blocks. The triangles on the x-axes locate the frequency of $1/(2FI)$.

ment. We hypothesized that, if oscillations simply require time in extinction, then increasing the extinction segment considerably would increase the number of pigeons oscillating during the first extinction segment. Alternatively, it could be the case that reliable, well-defined pause–peck oscillations require the alternation of reconditioning and re-extinction periods. Therefore, in Experiment 2 we reproduced the FI (or VI in the control groups) training of Experiment 1, and then exposed the pigeons to one long extinction segment.

Results showed that, during the first extinction session, birds in FI groups responded continuously during a long interval, roughly 10 times the FI value, but then changed from this sustained pecking pattern to an alternation of pauses and pecks. The DFT analysis, performed on successive blocks of extinction, revealed that the pause–peck oscillations were related to the FI parameters. Birds exposed to 16 s or 48 s interfood intervals displayed oscillations with periods close to or slightly greater than 16 s or 48 s, respectively. In contrast, the VI pigeons pecked almost continuously during the extinction segments, as they had done during the food

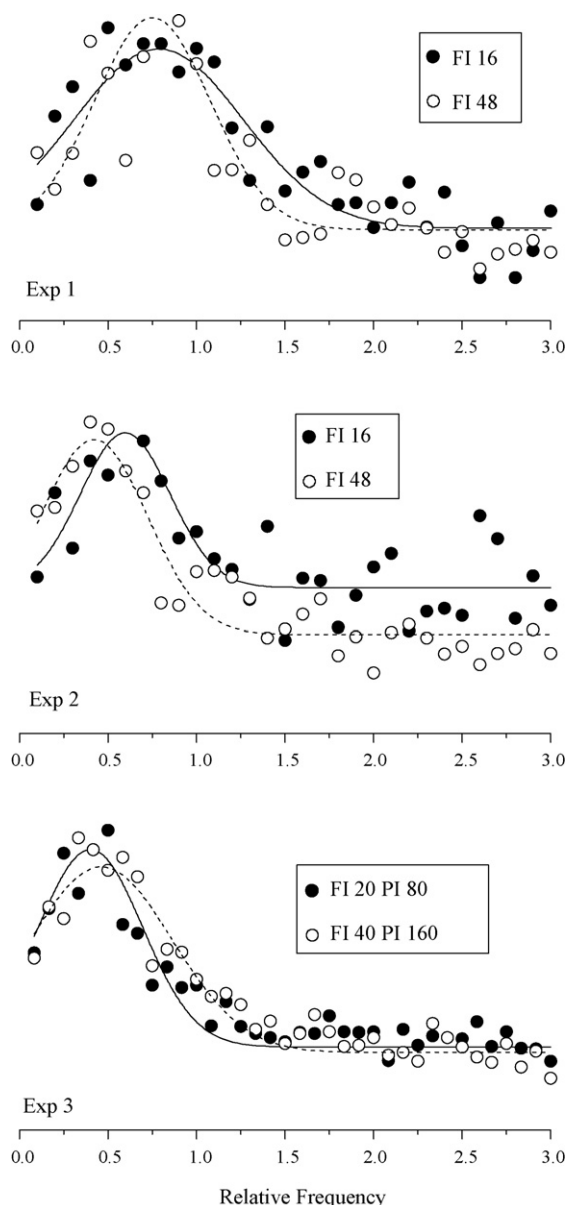


Fig. 15. Average data of the FI groups from the three experiments. All frequencies were divided by the reinforcement frequency of the group (in Experiments 1 and 2: 1/16 s for the FI 16 group and 1/48 s for the FI 48 s group; in Experiment 3, 1/20 s for the FI 20 s PI 80 s group and 1/40 s for the FI 40 s PI 160 s group). A four-parameter Gaussian function was fitted to each data set in order to estimate the frequency with the highest energy. The function had equation $y(f) = a + b \exp(-0.5 \times (f - \mu)^2 / \sigma^2)$, where f stands for relative frequency, and a , b , μ , and σ are free parameters. The function reaches its maximum value when $f = \mu$.

trials. The DFT analysis for the VI groups showed energy dispersed over a large range of frequencies, without any clear concentration on a specific frequency.

The results from Experiment 2 partly replicate with pigeons the results obtained by Crystal and Baramidze (2006) with rats. The data analysis showed, in two ways, that the response rate oscillations present during the extinction segment were related to the food periodicity. First, no such periodicities were observed in the VI groups, a result that implies that food deliveries with the same average interfood interval, but without periodicity, do not induce rate oscillations reliably. And second, because the periods of the FI 16 s and FI 48 s groups differed, it follows that the period of the oscillations is related to the period of food. However, the pause–peck

cycles were less clear than the ones found in Experiment 1 and, in contrast with Crystal and Baramidze's (2006) study, they did not occur since the onset of the extinction segment. The differences between our results and those of Crystal and Baramidze in the onset of the oscillations may be due to differences in the animal species, pigeons vs. rats, but why these differences occur at all remains to be explained.

The results from Experiments 1 and 2 question some descriptions of extinction following FI training. For example, before they start pausing, pigeons respond continuously for periods longer than the value mentioned by Gallistel (1990), that is, three or four times the FI parameter. Gallistel (1990) also states that during FI training pigeons form aperiodic representations of the interfood interval, but his conclusion seems at odds with the data presented above, namely, that (a) oscillations are present during extinction; (b) they require periodic food (cf. FI vs. VI groups) and (c) their period is related to the FI parameter (cf. FI 16 s vs. FI 48 s). In the same vein, our data also question the graphical representation of extinction after FI training, first proposed by Reynolds (1968) and subsequently reproduced in other textbooks (e.g., Blackman, 1974; Domjan, 1998; Millenson and Leslie, 1979; Walker, 1996). Scalloping or, perhaps more accurately, break-and-run patterns occur much later than suggested by Reynold's figure and they are not as reliable and clear as the figure seems to imply.

Although oscillations were observed in Experiments 1 and 2, there were hints that reconditioning and re-extinction may be critical for the quality and reliability of pause–peck cycles in extinction. Perhaps to oscillate the pigeon needs to learn not only when to start responding to collect food at $t = \text{FI}$ s into the trial, but also when to stop responding once t is appreciably greater than FI s. According to the hypothesis, in Experiment 1 oscillations were somewhat clearer and, after a few sessions, occurred earlier in the extinction segment than in Experiment 2 because successive sessions provided more opportunities to learn to start and then to stop responding. Oscillations were not as clear in Experiment 2 because the subjects had fewer opportunities to learn to stop responding. Therefore, in Experiment 3 we used the peak procedure because this procedure includes, in each session, periods of reconditioning (FI trials) and extinction (PI trials). After steady state performance was reached, we introduced at an unpredictable moment a long extinction segment, which is similar to a PI trial in all respects except duration.

If our hypothesis was correct, then we should observe oscillations since the beginning of the extinction segment, and these oscillations should be clearer and sharper than in Experiments 1 and 2. The results were consistent with the hypothesis. First, the pigeons showed pause–peck cycles immediately after the extinction segment started or very soon thereafter. Second, the cycles were displayed for intervals of time substantially longer than in the first two experiments (e.g., 720 s for the FI 20 s PI 80 s group or 1920 s for FI 40 s PI 160 s group; see Figs. 12 and 13). Third, in addition to the cumulative records, the power spectra also showed that the pause–peck cycles had periods related to the FI parameter. In the FI 20 s PI 80 s group, the oscillations had period close to 40 s, whereas in the FI 40 s PI 160 s group they had period close to 80 s. These periods are consistent with the idea that during the extinction segment the pigeons behaved as during the PI trials. That is, they started to respond around 1/4 to 1/2 of the FI, reached a maximum rate at $t = \text{FI}$ s, paused at $t = 2\text{FI}$ s, and resumed pecking afterwards. This pattern could be described as a 40-s cycle for an FI 20 s PI 80 s bird, and as an 80-s cycle for an FI 40 s PI 160 s bird. Fourth, although the cycles observed during extinction were similar to the cycles observed during the PI trials, for some pigeons the cycles became clearer in extinction (e.g., see Fig. 12, P013 or P284).

At a general level, the results from Experiments 1–3 suggest that two seemingly unrelated phenomena – response oscillations in the

peak procedure and performance in extinction following FI training – may be intimately related. At a more specific level, they may shed light on a puzzling set of findings reported in the literature. On the one hand, Kirkpatrick-Steger et al. (1996) found two response rate peaks during the PI trials when the FI and PI trials were in a 1-to-4 ratio. The authors suggested that these peaks could be due to an endogenous oscillator. On the other hand, Sanabria and Killeen (2007) did not find double peaks, but an increase in response rate till the end of the trial – a ramp. Following Roberts (1981) and Church et al. (1991), the authors interpreted the ramp as an anticipation of the next reinforcer and explained the differences between their findings and those of Kirkpatrick-Steger et al. (1996) in terms of procedural differences related to the time markers that signaled the trial onset.

However, the differences between the two studies – double peaks vs. ramps – may be more apparent than real. As we illustrate below, our data suggest that the ramp may be the outcome of averaging response rate curves that are in different phases and, more important, rate curves that, if prolonged, would reveal multiple peaks. That is, Sanabria and Killeen may have not seen rate curves with double peaks because the curves were truncated by the end of the PI trials. Prolonging the PI trials (as in our extinction segments) would have shown (slightly delayed) response rate peaks.

Fig. 16 illustrates the foregoing interpretation with a particularly compelling case, the data from pigeon P132, Experiment 3, group FI

40 s PI 160 s. The top panel shows two response rate curves obtained from averaging PI trials. The filled circles show the average of the 10 PI trials from the last session of Phase 2, that is, when all trials were either FI or PI trials. Average response rate increases from 0 to ~40 s, decreases from ~40 s to 80 s, and then increases until the end of the trial, revealing a typical ramp. The empty circles show the average of the last three PI trials from the first session of Phase 3, that is, just before the beginning of the extinction segment. Although with some delay, the same trend is observed, a peak followed by a ramp.

However, the analysis of trial-by-trial data revealed that the ramps stemmed from averaging step functions (i.e., pauses followed by roughly constant response rates) with the moment of the step occurring at different times into the trial. But, even more important, the ramps do not predict response rate during the extinction segment. The middle panel shows that rate (in bins of 4 s) during the first 1440 s of extinction (three blocks of 480 s each). After the first peak, a pause follows, and then response rate increases again. At 160 s, the duration of a PI trial, response rate is still increasing, which is consistent with the ramp in the top panels, but shortly thereafter response rate decreases, and then it clearly oscillates for more than 8 min (480 s). These oscillations are also visible in the cumulative record shown in the bottom panel (for the corresponding power spectra, see Fig. 13). In summary, we suggest that the ramps observed at the end of PI trials may be due to the averaging of the left limbs of the second response rate peaks, which

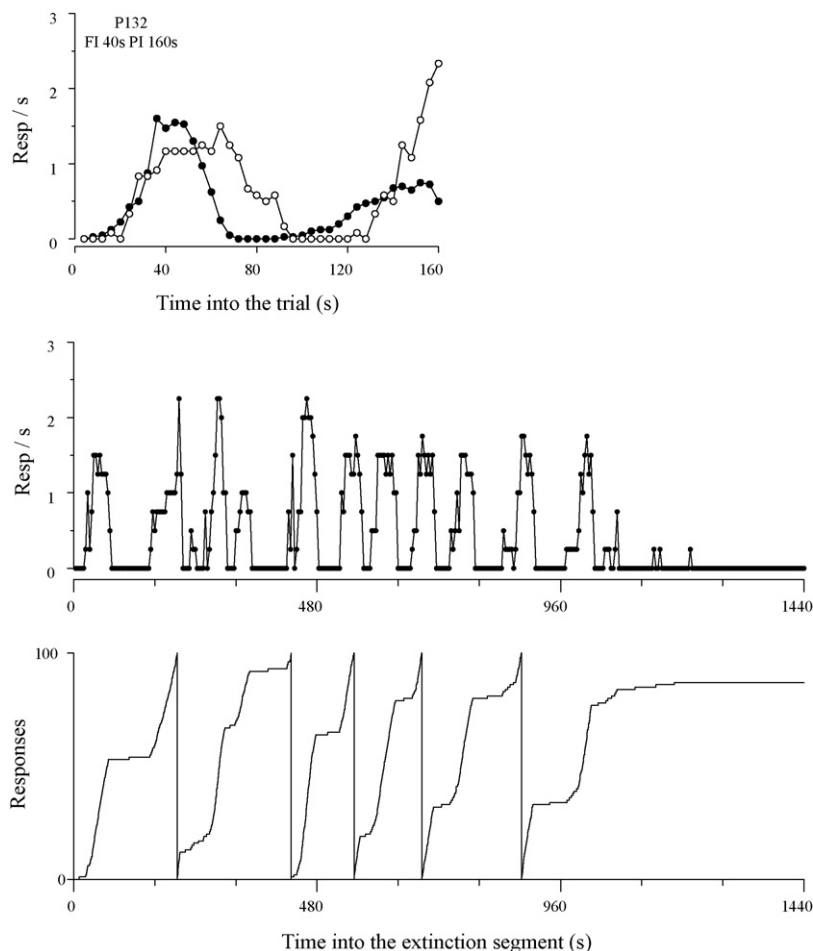


Fig. 16. Data from one pigeon (P132) from Experiment 3, group FI 40 s PI 160 s. Top panel: average response rate (in bins of 4 s) during the 10 PI trials from the last session of Phase 2 (filled circles) and during the last 3 PI trials from the first session of Phase 3 (empty circles). Middle panel: response rate (also in bins of 4 s) during the first 1440 s of the extinction segment. Bottom panel: corresponding cumulative record.

peaks are not revealed in their entirety simply because the end of the FI trial prevents it.

A theoretical consequence of the preceding interpretation is that the rate oscillations (and hence the ramps) have little to do with the anticipation of the next reinforcer. In fact, it would be difficult to see how anticipation could explain why some pigeons in Experiment 3 oscillated for more than 8 consecutive minutes, an interval of time much longer than the longest inter-reinforcement interval experienced during training, or why oscillations occurred at all in Experiments 1 and 2. Returning to the apparent inconsistencies between Kirkpatrick-Steger et al.'s (1996) results and Sanabria and Killeen's (2007) results, our findings suggest that the key issue is not 'When will ramps as opposed to double peaks occur?' but 'When will double peaks occur immediately as opposed to with a delay?'

Why do pigeons display pause–peck cycles in extinction? One obvious hypothesis involves the activation of a self-sustaining endogenous oscillator (Church and Broadbent, 1990; Kirkpatrick-Steger et al., 1996; Crystal and Baramidze, 2006). Because the pause–peck cycles have periods related to the FI parameters, the endogenous oscillator could have been entrained by successive food deliveries and then modulated response rate variations. However, the oscillator hypothesis has difficulties explaining why the oscillations in Experiments 1 and 2 did not start immediately at the onset of extinction and why they lasted only a relatively short period of time.

Another hypothesis conceives of the oscillations as the outcome of a dynamic, learning process. According to this hypothesis, the pigeons would learn when to start responding and, under some circumstances, also when to stop responding. In extinction following the FI training, the pigeons initially would respond at a steady rate because they had had no opportunity to learn to stop responding. Some pigeons would learn to stop during the first extinction segment and then, whenever they stopped, they would put themselves in a situation similar to the onset of a regular FI trial. That situation would function as a cue to another cycle of pecking followed by a pause (for similar ideas, see Ferster and Skinner, 1957, Chapter 5; Morse, 1966). Other pigeons would require a few sessions to learn to stop and therefore, for these pigeons, the oscillations would not start immediately. Still according to the hypothesis, in Experiment 3, the two dynamic effects mentioned above would have had ample opportunity to develop and fine tune their temporal properties in interaction with the reinforcement contingencies. Hence, the oscillations would occur immediately at the onset of extinction and for long stretches of time. It is also conceivable that both hypotheses are partly correct in that the start and stop learning processes and their temporal properties could rely on the output of an endogenous oscillator. Clearly, the process or processes underlying behavioral oscillations and the conditions in which they are engaged remain to be investigated.

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