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Behavioral adjustment to modifications in the temporal parameters of the environment

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Abstract

We study the dynamics of behavioral transitions when European starlings (*Sturnus vulgaris*) experience stepwise changes in the value of a meaningful time interval. Subjects were primed to respond at a certain time T_1 . After extensive training, the primed time changed to a new value T_2 . In Experiment 1 subjects were reinforced on 40% of the trials and they experienced a single transition which lasted until asymptotic behavior was reached. Starlings showed a progressive adjustment to T_2 , with no obvious discontinuities. In Experiment 2, probability of reinforcement was initially 20%, and the schedule switched to extinction after a varied number of trials were reinforced at the post-transition time. The number of post-transition reinforcements was used as independent variable. Behavior was examined in extinction to judge the state of temporal performance after a controlled amount of experience. Under these conditions, adjustment to T_2 took place in two stages, and there was an intermediate phase when behavior changed little. These results are consistent with the hypotheses that animals continuously update the subjective probabilities that reinforcement comes at any given time and that responding occurs when the current estimate is above a certain threshold. We show that in spite of the continuous updating of time estimates, responding can show either continuous or discontinuous adjustments depending on the vicinity of the pre- and post-transition times and the probability of reinforcement. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Behavioral timing includes two classes of phenomena, periodical or rhythmic timing and interval timing. The former allows organisms to tune their activity to regular environmental contingencies such as daily or seasonal fluctuations in op-

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portunities or predation risks; because the relevant periodicities are similar across generations, the periods of the cycles can be coded genetically, leaving the phase adjustment to individual experience. Interval timing, in contrast, concerns the adjustment of behavior to the elapsed time between arbitrary events, and hence the length of the intervals has to be learned.

Given that the need for learning is a diagnostic feature of interval timing, it is paradoxical that the process of learning about time intervals, that is, the dynamics of how behavior becomes tuned to specific interval lengths, has been largely neglected in the timing literature. The two predominant theoretical approaches to animal timing, Scalar Expectancy Theory (SET, Gibbon, 1977; Gibbon and Church, 1984; Gibbon et al., 1984) and Behavioral Theory of Timing (BeT, Killeen and Fetterman, 1988) address behavior at the steady state, when subjects, having experienced a given interval repeatedly, have acquired a stable response pattern.

The study of the dynamics of behavioral adjustment to temporal properties of the environment has remained, with few exceptions, only marginally connected to mainstream theoretical approaches. It has proceeded along various lines, but we refer here only to a few approaches that are specially relevant to the present study (for an example of important work on dynamics which we will not address see Mazur (1997)). Meck et al. (1984) trained rats according to a peak procedure (Catania, 1970; Roberts, 1981). In every reinforced trial, subjects received a stimulus and the first response after a pre-determined interval had elapsed resulted in a food reward. Rats normally start responding before the typical time of reinforcement and keep responding until food is obtained. Intermingled with these reinforced trials, however, there were empty trials in which no reinforcement occurred. Typically, in an empty trial an animal starts responding as in normal trials and stops some time after reward should have occurred. The pattern of responding in these empty trials (the times at which responding starts and stops, and the central or 'peak' value between these extremes), is a measure of how behavior is tuned to the normal time of reward. To study

dynamics, Meck et al. (1984) introduced an un signaled change in the typical timing of reward (from 10 to 20 s for a group of rats, and from 20 to 10 s for another group) and examined how response patterns changed with experience. They report that after the transition in reward time their subjects maintained their original pattern for a number of trials, then jumped to a new phase in which the peak of responding occurred close to the geometric mean (square root of the product) between the old and new intervals, and finally jumped again to the post-transition interval.

Lejeune et al. (1997) extended the experimental procedure used by Meck et al. (1984) by exposing the rats to different times of reinforcement and using different proportions of reinforced trials. Although Lejeune et al. (1997) report two-step transitions in one of their experimental conditions, their most common finding is a gradual modification of the timing of the peak of responding during downward transitions (new reinforced time shorter than the previous reinforced time), and an abrupt increase in the time of the peak of responding after a single reinforcer at the new criterion, followed by a gradual approach to the asymptotic criterion, during upward transitions. Lejeune et al. (1997) explain their basic findings in terms of a hierarchical model: at the top level, rats must identify the temporal dimension as being the one correlated with reinforcement. This may take a large number of trials, but it needs only be done once at the start of the experiment. When the time to reinforcement changes, only the new time to reinforcement has to be learned. This, they argue, can be done using an exponential weighted moving average (EWMA), of the sort modeled by Killeen (1981). But, as Lejeune et al. (1997) recognize, this approach fails to explain the appearance of two-step transitions in some conditions. Furthermore, they state that the dependence of two-step transitions on the parameters of the experimental conditions 'provides another theoretical problem untreated by the EWMA model or, indeed, by any others' (229 pp.).

A different approach of immediate relevance for our study is that favored by Staddon and co-workers (for recent developments and references to this literature, see Higa, 1997a,b). These

researchers have exposed rats and pigeons to response-initiated delay and fixed-interval schedules, and have studied the effect of modifying the inter-food interval (IFI) on the wait time (time elapsed between a reinforcement and the next response). As a general rule, wait time changes as soon as the IFI is modified. But there are some complications: the adjustment in wait time depends on the actual values of the IFIs, it can continue gradually after the initial jump, and it proceeds faster in downward than in upward transitions (exactly the opposite effect from the one reported by Lejeune et al., 1997). No two-step transition in wait time has, to our knowledge, been reported to date. Research on the adaptation of waiting times has generated a number of models, based on the idea that waiting times are determined by the IFI's during the last few trials, with shorter IFI's having a disproportionate effect (Higa, 1996; Wynne et al., 1996).

Comparison of the results obtained by Meck et al. (1984) with those of Higa (1997a,b) and Lejeune et al. (1997) is difficult because of procedural differences and also because of the treatment of the data: while Meck et al. (1984) report two-step transitions in individual data, later work has reported group averages (Lejeune et al., 1997) or individual average values over several sessions (Higa, 1997a,b). As pointed out by Meck et al. (1984), the average of several two-step transitions will be a continuous transition unless all the steps are positioned on the same trial. While a discontinuity on the average data will always reflect a discontinuity in the individual data (the average of continuous functions is also continuous), the reverse is not necessarily true: discontinuous individual transitions may hide behind continuous averages.

Yet another line of previous work on dynamics of time perception which connects with our interests here is that pursued within the scope of optimal foraging theory. The rationale underlying this work is exemplified by work that uses the framework of the Marginal Value Theorem (MVT, Charnov, 1976). The situation often considered is that of a consumer who exploits patchily distributed food. The patches are assumed (or programmed) to deliver diminishing

returns on each visit (normally this implies increasing intervals between prey captures), and some known travel cost (again, often described as a time lost to food collection) that must be incurred to switch between patches. This task is very different from the previous ones because the subjects are not expected to behave as if pursuing an accurate reproduction of the typical time of reinforcement. Instead, the dependent variable of interest is the initiation of patch switches. Because patches deplete, it comes a point in each cycle where the subject benefits by leaving the present patch and traveling to a new one. The point at which this occurs (that is the degree of depletion tolerated before a switch) depends on the subject's expectation of forthcoming travel time: the longer the expected travel time the greater the tolerance to depletion. Researchers in this area have studied the dynamics of tolerance to depletion (patch time) as a function of temporal manipulations of travel time (Kacelnik and Todd, 1992; Todd and Kacelnik, 1993; Cuthill et al., 1994). Of special relevance here is the work of Kacelnik and Todd (1992) and Todd and Kacelnik (1993) which used various mixtures of travel times to uncover the process by which patch time responds to recent travel experience. They found that accommodating the data required assuming sensitivity to both the most recently experienced and the longer term average of travel times, and suggested a model that combined the assumptions of SET for the structure of reference memory, the decision rule suggested by optimal foraging theory and a dynamic algorithm for updating of time estimations.

In this paper we report the results of two experiments in which European starlings (*Sturnus vulgaris*) were exposed to a sudden modification of the reinforcement time in a variant of the peak procedure and then examine our results, together with those from several of the studies described above, within the framework of theoretical accounts of behavioral timing. In particular, we examine if a variation of the model proposed by Todd and Kacelnik (1993) for the MVT with a decision rule that reflects the logic of the peak procedure can generate both the continuous and discontinuous (two-step) transitions obtained in this kind of experiments.

2. Experiment 1

The first experiment combines the protocols used by Meck et al. (1984) and by Brunner et al. (1992). Starlings were trained in a peak procedure and, after extensive training, the time to reinforcement was changed from 20 to 10 s in stepwise fashion. In contrast with the procedure used by Meck, Komeily-Zadeh and Church, trials were initiated and terminated by the subjects, as was the case in Brunner, Kacelnik and Gibbon's experiment. This modification of the standard peak procedure design ensures that the birds are attentive to the beginning of the trials and to some extent standardizes motivational state, because trials are spaced by the animal itself, reflecting their willingness to work for reward. The procedure also yields two additional measures of performance, the time of cessation of responding before a patch switch and the time of initiating the switch itself.

2.1. Methods

2.1.1. Subjects and apparatus

Six adult starlings, wild-caught and experimentally naive, were used for the experiment. They were kept in two indoor aviaries, at 18°C and with a 13L:11D light-dark cycle (dawn at 06:30, dusk at 19:30 h), in individual cages measuring 140 × 40 × 45 cm³. The subjects could not see one another, but they were in auditory contact. Birds received ad libitum turkey crumbs from 13:00 to 15:00 h and six mealworms at 17:30 h when they were weighed and were food deprived till the beginning of the following session. There was free access to drinking water at all times and a bathing bowl was supplied at the end of the experimental session.

The experiments were conducted in the home cages. Each cage had a patch panel in the center of the back wall with a 4 × 5 cm² flapping door covering a food hopper. This door was in a plane at 30° with the horizontal and could be illuminated from behind with a green patch light. The food hopper was connected to a pellet dispenser (Campden Instruments) filled with turkey crumbs sieved to an approximately even size. The stan-

dard reward consisted of 15 units of crumbs (mean weight of 0.18 g, S.D. = 0.0216 g; Bateson, 1993). Rewards were signaled by audible clicks from the pellet dispenser and by a red light next to the food hopper. A patch perch, 15 cm high and 25 cm long, with a white patch light above it, was situated opposite the food hopper. Two travel perches were situated on either end of the cage, 120 cm from each other and 11 cm above the floor of the cage. Each perch was connected to a microswitch which registered the presence (switch on, perch lowered by ca. 1 cm) or absence (switch off, perch in rest position) of a starling on the perch. A 'hop' was operationally defined as a transition from the off to the on state of the microswitch following an off state longer than 0.25 s. (This restriction was imposed to ensure that starlings could not operate the switch by small hops on the perch itself: instead, they had to leave the perch during at least 0.25 s. In practice, starlings hopped on the perch from the floor or flew to and from the cage wall.) There were two white travel lights situated on the end walls of the cage, 30 cm above the floor. An Acorn A5000 microcomputer running ARACHNID experimental control language (Paul Fray Ltd.) controlled the stimulus events and response contingencies as well as recording the data from an adjacent room.

2.1.2. Training and experimental procedure

Starlings were first shaped to hop on the patch perch. Every hop on the patch perch while the patch light was illuminated was rewarded with a food delivery. The patch light was then switched off for the duration of the inter-trial interval (ITI). We used hopping onto a perch, rather than the more usual key pecking as a response to make sure that the response had non-negligible energetic cost, hence promoting selectivity in the timing of response emission. After three sessions, trial initiation was introduced. All lights (except for house lights) were switched off during the ITI. At the end of the ITI, the travel lights were switched on. As soon as the subject hopped on a travel perch, the travel lights were switched off and the patch light was switched on. After *n* hops on the patch perch, the patch light was switched off, food was delivered and a new ITI started. In

the following three sessions the number of hops required to obtain food was 6, 9 and finally random with mean 14, respectively.

In the next phase the starlings were exposed to the peak procedure. Food deliveries followed, with probability $P = 0.4$, the first hop after 20 s had elapsed from the initiation of the trial. Non-reinforced (empty) trials ended after 60 s. The ITI was 90 s. The sequence of reinforced and empty trials was random. If a trial was scheduled to be reinforced at time T (which in a later stage changed from 20 to 10 s as explained below), the bird received the reward only if it produced a response between times T and $1.25 \cdot T$. This ensured that the starlings were never reinforced at times much larger than the scheduled ones. Finally, subject-terminated trials were introduced after one month of training in the peak procedure. The final schedule was thus as follows: at the end of the ITI the travel lights were switched on. As soon as the starling hopped on a travel perch; (i) time to food delivery started to elapse; (ii) the travel lights were switched off and (iii) the patch light was switched on. The travel lights were switched on again after the starling hopped once on the patch perch. In reinforced trials, the first hop on the patch perch after a time T had elapsed was rewarded with food, provided that no more than $1.25 \cdot T$ s had elapsed from the beginning of the trial. Trials ended when food was delivered or when starlings hopped on a travel perch. A diagram representing the structure of the trials is presented in Fig. 1.

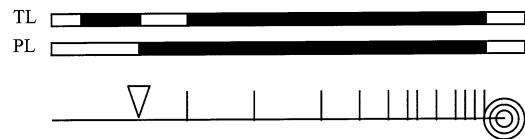
Sessions were run 7 days per week. They started at 07:00 h and ended after 4 h or when 200 trials were completed, whatever came first. For each trial, the computer recorded the time (in centiseconds) from one hop to the next and the duration of the trial. After 2 weeks of data collection, the time to reinforcement in rewarded trials was changed from 20 to 10 s, everything else remaining equal. After 1 more week, the experiment finished. The results from the 5 days preceding and following the transition were used for the analysis.

2.2. Results

2.2.1. Molar analysis: effect of condition

To study the effect of reinforcement time, we calculated for each bird the average value (over the last three sessions of each condition) of the latency to respond (time from the start of the trial to the first hop on the patch perch), median response time, time of the last response (giving in time, GIT) and duration of the trial (moving on time, MOT). Although response latencies were longer in the 20 s (average \pm S.D.: 5.06 ± 1.28 s) than in the 10 s (3.79 ± 0.14 s) condition, the difference was not significant ($t_5 = 2.46$, $P = 0.057$). Reinforcement time affected median response time (before: 18.92 ± 0.95 ; after:

Reinforced trial:



Empty trial:

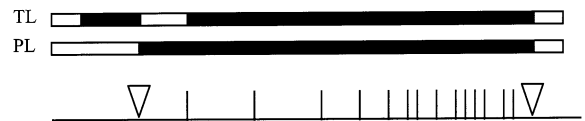


Fig. 1. Schematic representation of the experimental contingencies during a reinforced (top) and an empty (bottom) trial. For each trial type, the shaded portions of the uppermost bar indicate when the travel light (TL) was switched on. Shaded portions of the following bar indicate when the patch light (PL) was switched on, and symbols on the bottom line indicate responses of the subjects. An inverted triangle indicates a hop on the travel perch and a vertical line a hop on the patch perch. The start of a new trial was indicated by the TL being switched on. As the bird hopped on the travel perch, the TL was switched off and the PL was switched on. The TL was switched on again (indicating that the bird could leave the patch and search for a new one at any time) upon the first response in the patch. On reinforced trials, the first hop on the patch perch after the FI had elapsed (20 s in the initial phase of the experiment, 10 s in the final phase) was reinforced (indicated by the concentric circles) and both lights were switched off for the duration of the ITI. On empty trials, patch responses were never reinforced and the birds had to terminate the trial by hopping on a travel perch.

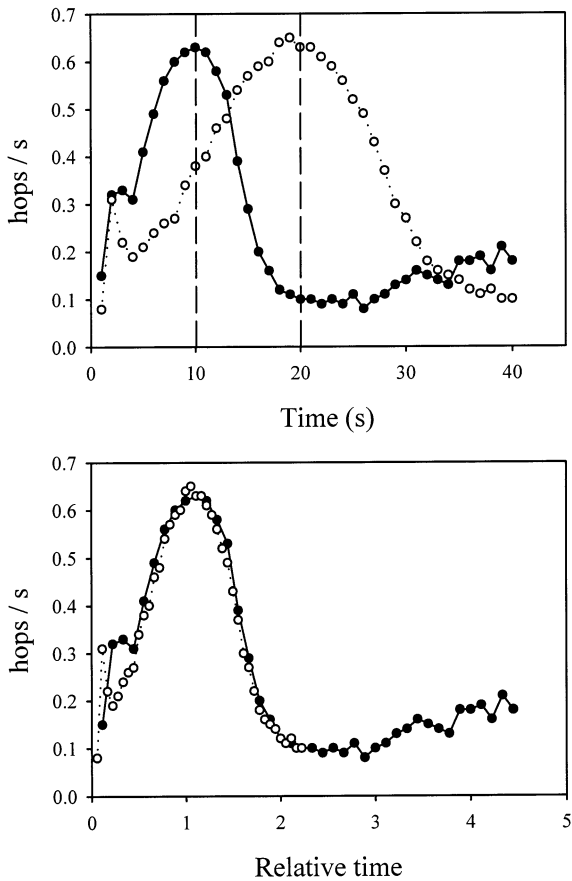


Fig. 2. Response rate (number of hops per second) before (○) and after (●) the transition plotted vs. time in the trial (top) and time relative to the time of maximum response rate (relative time, bottom). Observe the superposition of response rates when plotted vs. relative time. In the top panel, the time of reinforcement before and after the transition is indicated by dashed vertical lines for reference.

11.31 ± 1.35 ; $t_5 = 12.11$, $P < 0.0001$), GIT (before: 32.81 ± 3.91 ; after: 22.60 ± 5.31 ; $t_5 = 4.39$, $P = 0.007$) and MOT (before: 43.50 ± 5.56 ; after: 29.86 ± 6.46 ; $t_5 = 5.45$, $P = 0.003$).

Average response rates during the last 3 days of each condition (Fig. 2) show two important features, characteristic of the peak procedure (Roberts, 1981): the peak of response is placed at, or close to, the time of reinforcement and, when response rates are plotted as a function of time relative to the 'peak time', they closely superimpose—a clear example of the scalarity of timing.

2.2.2. Molecular analysis: transition effects

In view of the results of the molar analysis, the effects of the transition were investigated on the peak time (related to median response time and defined below). Response latencies were too noisy to show a consistent pattern. Of the three measurements that differed between the two conditions, it has been shown in a different setup that the MOT is not a good indicator of the subject's timing abilities, since it is affected by motivational factors unrelated to reinforcement time (Kacelnik et al., 1990; Brunner et al., 1992). From the remaining two candidates, we selected peak time for further study because of its lower variability in constant experimental conditions.

We used two methods to identify the peak time (Rodríguez-Gironés, 1995). One of them looked for the maximum likelihood estimators of the break points in an analogue of the break-run-break analysis used by Gibbon and his collaborators (Gibbon and Church, 1992; Church et al., 1994; Leak and Gibbon, 1995). The other one searched for the point of maximum deflection in the cumulative plot of responses vs. time. Because the results of both methods were highly correlated ($R^2 = 0.974$, $P < 0.0001$), only the analysis of the peak time as calculated with the maximum likelihood approach will be presented.

The adjustment of the peak time to the new environment can be seen in Fig. 3. Although the data for bird 4 presents a discontinuity between the pre-transition and the asymptotic post-transition peak time, other graphs seem to correspond better to a smooth transition. A non-parametric test can be used to study whether the adjustment of peak time proceeded in two (or fewer) steps. The basic idea of this test (described in Appendix A) is as follows: let $d_i = t_i - t_{i-1}$, where i is the number of trials since the modification in reinforcement time. If the adjustment of peak time proceeds in two steps, there should be two large negative values of d_i (corresponding to the two downward steps), and the rest should be randomly distributed: since the number of negative values of the d_i exceeded the number of positive values by more than two ($G_p = 4.428$, $DF = 1$, $P < 0.05$), and there were no differences among birds in this respect ($G_h = 0.711$, $DF = 5$, $P =$

0.98), we can reject the null hypothesis that the adjustment of the peak time proceeded in two steps.

2.3. Discussion

The hypothesis of a two-step adjustment can be rejected at the 5% level of significance. This does not imply a continuous transition (in all rigor, it makes little sense to talk about continuity when behavior is recorded as a series of discrete points), all it implies is that the adjustment to the new criterion takes place in three or more steps. To provide a better illustration of the smoothness of the transition, we have re-plotted the data from Fig. 3 by pooling empty trials in blocks of ten, and calculating the peak time for each block

following a variation of the method proposed by Meck et al. (1984), which makes no assumption about the pattern of responses. The method works as follows: we counted the number of responses (averaged over the ten trials) in each 3 s interval (1–3, 2–4, . . .) and identified the interval(s) that contained the maximum number of responses. The peak time was defined as the median time of the responses comprised between the start of the first such maximum response interval and the end of the last one. Fig. 4 shows the results of such a procedure, after smoothing the data with a 5R digital filter. This filter works as follows. Let t_i be the peak time in the i th trial, and m_i the median value of $\{t_{i-2}, t_{i-1}, t_i, t_{i+1}, t_{i+2}\}$. The filter substitutes, for all i , the median m_i for the trial value t_i , a process that is iterated till

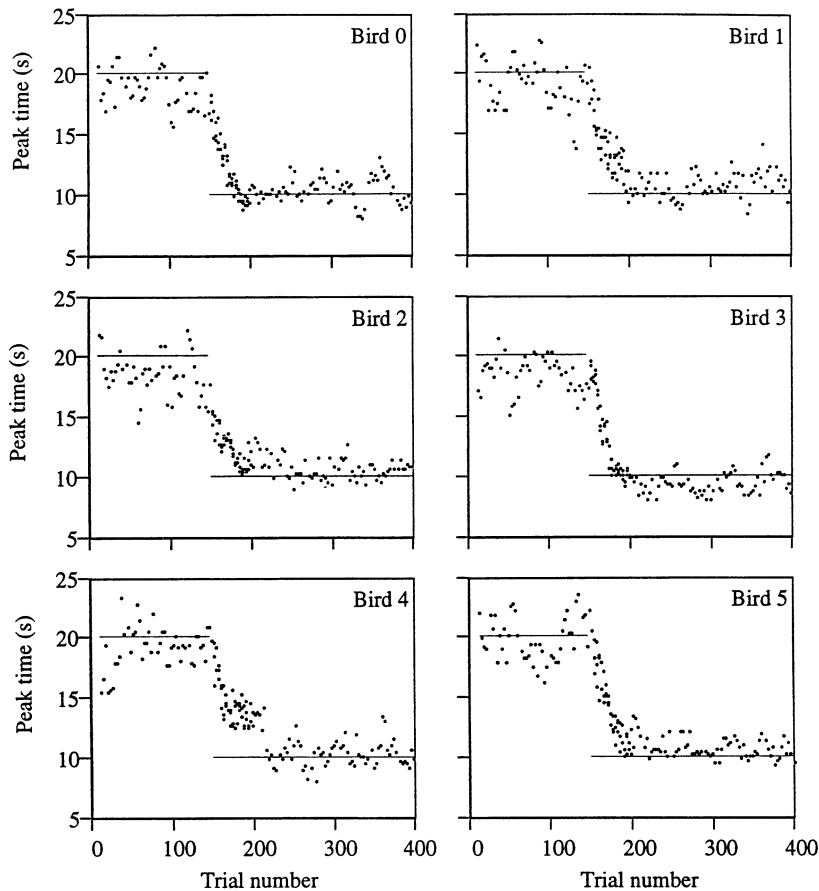


Fig. 3. Modification of the peak time in response to the stepwise change of time to reinforcement.

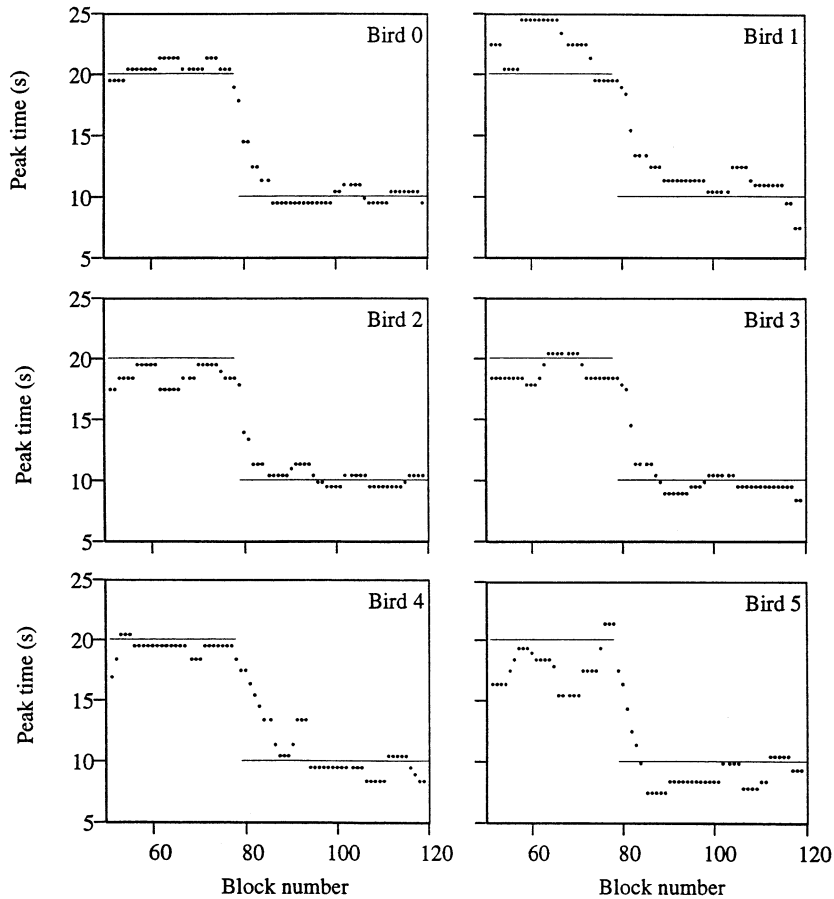


Fig. 4. Smoothed peak time calculated from blocks of ten trials. The time of reinforcement is plotted as a continuous line for reference.

convergence. (For details and a discussion of possible caveats see Meck et al., 1984.)

As it can be seen in Fig. 3, there were oscillations in the value of peak time. An exploratory statistical analysis failed to detect any daily pattern that might be responsible for these oscillations.

We also attempted to investigate upward transitions in peak time. However, the use of subject-terminated trials made impossible the study of a $10 \rightarrow 20$ s transition because subjects left the patch before reinforcement was due and, instead of experiencing the scheduled $10 \rightarrow 20$ transition they experienced a $10 \rightarrow$ extinction $\rightarrow 20$ transition. For this reason, the results of a $10 \rightarrow 20$ transition that followed the $20 \rightarrow 10$ transition

described above are not reported here. Although it is disappointing to dismiss this data for the present purposes, it is worth noticing that the phenomenon we report has implications for the upward transitions reported in the literature: during the first few trials following an upward transition, individuals may be responding at very low frequencies at the time when the reward is scheduled. Because rewards are normally delivered following the first response produced after the scheduled time to reinforcement, the low response rate implies that the first post-transition rewards may actually be obtained at times much longer than the scheduled ones. In this respect, two points should be noticed. (a) The experienced delay to reinforcement is always greater than the

programmed one (when response rates are high, the differences are small but during transitions the difference can be substantial: the reinforcement is scheduled at a time when it is not expected and when response rates are usually low). This implies that in upward transitions subjects experience a greater shift than the one planned by the experimenter, and in downward transitions the experienced shift is always smaller than planned. (b) The difference between experienced and planned shifts in reinforcement is greater in an upward than in a downward transition. This result is due to the response pattern. Consider the asymptotic response rates in the present experiment when reinforcement came at 10 and 20 s (Fig. 2): When reinforcement was scheduled at 20 s, response rates at 10 s were lower than peak response rates, but still substantial (60% of peak response rates). On the other hand, when reinforcement was scheduled at 10 s, average response rates 20 s after the start of the trial were very low indeed (15% of peak response rates). The asymmetry reported by Lejeune et al. (1997)—adjustment is faster in upward transitions—might therefore reflect the difference between planned and experienced times to reinforcement. Indeed, in an experiment with upward and downward stepwise transitions in travel time in the context of the MVT, starlings showed perfectly symmetric adjustment to the change, taking about six cycles to reach asymptotic patch visiting time in both cases (Cuthill et al., 1994). In the MVT protocol the asymmetry in the relation between programmed and experienced transition does not occur.

3. Experiment 2

In Experiment 1 there were normally one or two empty trials between consecutive reinforced trials. Thus, for a certain amount of experience with the post-transition reinforcement time (i.e. for a certain number of trials reinforced at the post-transition reinforcement time), we had an average of 1.5 empty trials that we could use to probe the memory of the starlings. Experiment 2 was designed to increase the number of samples for a given amount of experience after a stepwise

change in input. Subjects experienced the same transition in reinforcement time (20 → 10) once per week. After a certain number of reinforced trials, N (that changed from session to session), reinforcement was interrupted for 30 trials. As a result, for each value of N employed, we had at our disposal 30 empty trials to probe the memory of the subjects. Therefore, this method gives a clearer picture of the starling's reference memory for a given amount of experience, but it does not allow to follow each transition until asymptotic behavior is reached.

3.1. Methods

Subjects were six adult wild-caught starlings, experimentally naive. They were kept in the same aviaries as those used for Experiment 1 and used the same panels that were used for Experiment 1. Training was as for Experiment 1, except that the reinforced response was a peck in the door covering the food hopper and the probability of reinforcement per trial was $P = 0.2$. The general conditions (food deprivation, length and timing of sessions, trial termination) were identical to those in Experiment 1. Sessions were divided in two groups: baseline sessions and transition sessions. In baseline sessions trials were reinforced with probability $P = 0.2$ after 20 s from the beginning of the trial. Transition sessions (Fig. 5) started as baseline sessions, but once the bird obtained 45- N

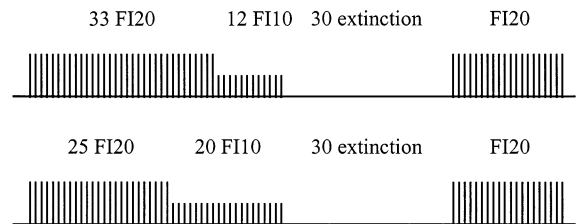


Fig. 5. Schematic representation of a transition session for $N = 12$ (top) and 20 (bottom). After 45- N trials reinforced at 20 s, the time to reinforcement was changed to 10 s for N reinforcers. These trials were followed by 30 consecutive empty trials (extinction trials) and the session ended with as many FI 20 trials as the bird managed to complete. In both the FI 20 and FI 10 conditions, trials were rewarded with probability $P = 0.2$. Reinforcers are represented by vertical lines, and the time of reinforcement by the height of these lines.

reinforcers (with $N = 0, 1, 2, 3, 5, 7, 9, 12, 15, 20, 25, 30$ or 35 in different sessions) the time to reinforcement was changed to 10 s. The probability of reinforcement remained at $P = 0.2$ until the bird collected N reinforcers at 10 s, at which point the probability of reinforcement was set equal to zero for 30 trials (thus, the 30 extinction trials always occurred after 45 reinforcers). After these 30 extinction trials the initial conditions were re-established, with reinforcement occurring at 20 s with probability $P = 0.2$. There was one transition session every Thursday. All birds received the $N = 0$ session during the first week to verify that they would keep responding for 30 extinction trials, and sessions with other values of N were scheduled following a modified Latin square design.

Responses during the extinction trials of the transition sessions were recorded as the number of responses (pecks) in each 1 s interval. Because bird 5 died after 4 weeks, its data will be shown in the figures but was not used for statistical analyses.

3.2. Results

Fig. 6 shows individual response patterns during the extinction trials for three values of N ($N = 0, 15$ and 35). Each curve represents the number of pecks produced per 1 s bin during ten consecutive empty trials (thus, average pecking rates are obtained dividing plotted values by ten). Response rates at the peak time in Experiment 2 (ca. 1.5 s^{-1}) were higher than in Experiment 1 (0.64 s^{-1} ; compare Figs. 2 and 6), as one could expect from the fact that hops on a perch are more costly than pecks, both in terms of time and energy. Response patterns are unimodal at all stages and show no consistent modifications as a function of time since the last rewarded trial. We therefore pooled, for each bird, the data from the 30 trials corresponding to a given transition session and calculated a single peak time from these 30 trials using the procedure explained for Fig. 4.

Fig. 7 shows how peak time decreased as the birds experienced an increasing number of pre-extinction rewards at 10 s. The peak time then stabilized before decreasing further. This trend

can be seen more easily by taking the average of the peak time across the different birds (Fig. 8). The non-parametric test described in Appendix A shows that the data from the five birds was homogeneous ($G_h = 0.527$, $DF = 4$, $P > 0.95$) and that the transition proceeded in more than two steps ($G_p = 3.97$, $DF = 1$, $P < 0.05$).

3.3. General discussion

In spite of large inter-individual variability, the pattern that seems to emerge from Experiment 1 is that, in response to a stepwise environmental transition, starlings adjust the timing of their behavior in a smooth fashion (Fig. 4). The results from Experiment 2, on the other hand, suggest that there is a small range of experienced new values after a transition for which behavioral modifications are basically at a halt (Fig. 8). This latter pattern is reminiscent of the two-step adjustment reported by Meck et al. (1984), but it should be remembered that adjustment to the new time of reinforcement proceeded in more than two steps: thus, although in Experiment 2 starlings adjusted their response time in two stages, each stage consisted of several small jumps.

There are some similarities between our results and those obtained by Lejeune et al. (1997) with rats. First of all, adjustments to the new time to reinforcement in downward transitions (such as the $20 \rightarrow 10$ transition reported in our experiment) proceeded gradually when the proportion of reinforced trials was elevated (40%, Experiment 1), and two-stage transitions appeared when the proportion of the reinforced trials decreased (20%, Experiment 2). Lejeune et al. (1997) report gradual transitions when the proportion of reinforced trials was 70%, and appearance of two-step transitions when the proportion of reinforced trials fell to 50%. Because of the many differences between the studies (including the use of different species), it may be fruitless to seek explanations for all differences in results, but we believe that the common finding that discontinuities in the transition became apparent at lower reward probabilities is interesting and may be accounted for by a theoretical model that we present below.

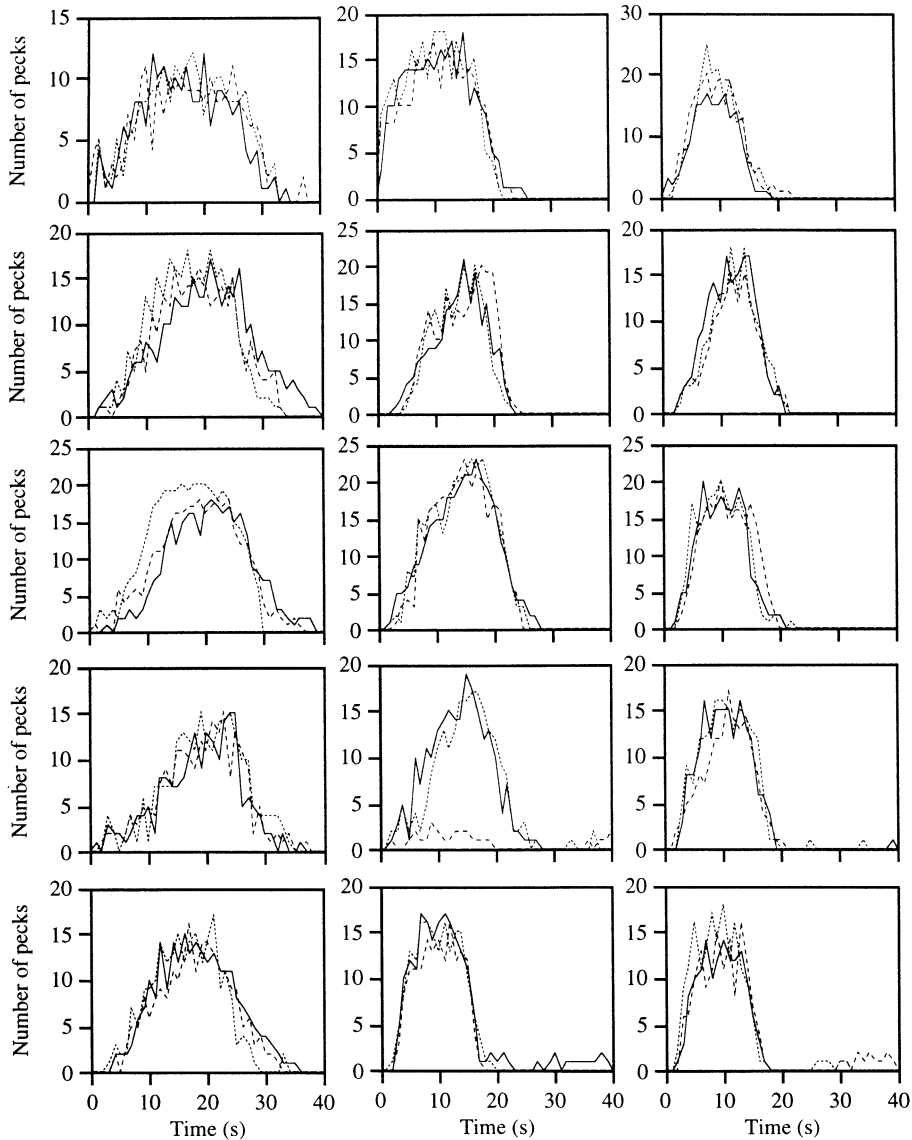


Fig. 6. Individual response patterns during extinction trials. Each panel represents, for one particular bird and N trials rewarded after 10 s, the number of pecks given in 1 s bins over the first (solid line), second (dotted line) and third (dashed line) blocks of ten extinction trials. Columns correspond to different values of N (from left to right, $N = 0, 15$ and 35) and rows to different birds (from top to bottom, 0 to 4). Bird 3 only finished 23 extinction trials with $N = 15$.

4. A conceptual model: subjective probability and optimal responding

To make a start in the development of a theoretical account for dynamics of responding in the peak procedure, we will focus on the hypothetical goal of responding. Our aim is not to

produce a rigorous model of the energy-maximizing behavior of starlings in the peak procedure. Instead, we will discuss qualitative aspects that the optimal response pattern may show under the constraints imposed by realistic assumptions on temporal information processing.

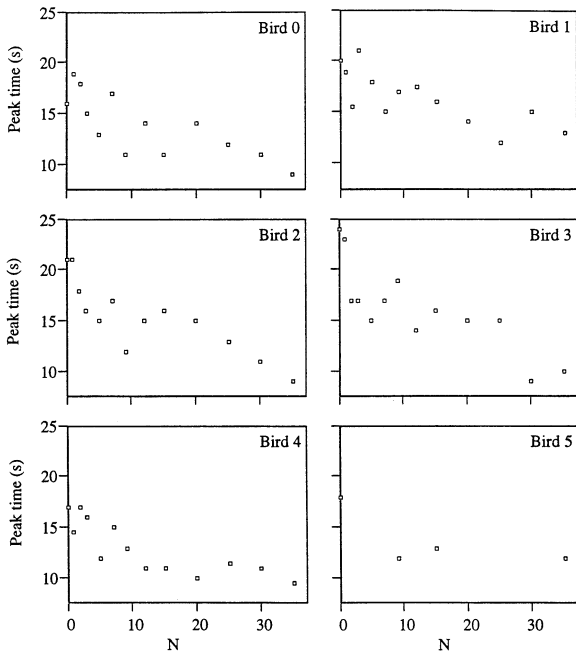


Fig. 7. Peak time vs. number of reinforcers (N) experienced after a transition from 20 to 10 s.

We assume that at each time t within a trial, the subject has some estimated probability of reinforcement, $P(t)$, which in general will be different from the scheduled probability. As a first approximation to the optimal policy, one can take the following family of rules: subjects respond whenever $P(t)$ exceeds some threshold, $P(t) > \beta$. By modifying the value of the threshold subjects can adjust to different experimental situations.

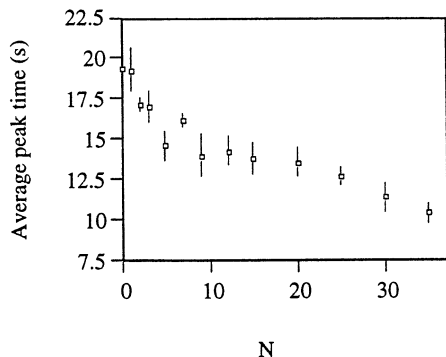


Fig. 8. Average peak time vs. number of reinforcers (N) at 10 s. Error bars are S.E.

The estimated reinforcement probability, $P(t)$, will depend on the pattern of variability in the 'clock' and in memory. Following SET, and the need to accommodate Weber's Law, we will assume that in the peak procedure $P(t)$ is a normal distribution, centered around the time of reinforcement, T , and with standard deviation proportional to T . The rule $P(t) > \beta$ will be satisfied for a period of time centered at T , and a 'peak time' in responding on a given trial would be identified as the center of this period.

As a preliminary to discussing transitions, we now consider a static situation where reinforcement can come at times T_1 with probability P_1 , and T_2 with probability P_2 (we will assume that $T_1 < T_2$ and $P_1 + P_2 < 1$). What is the optimal response pattern? Let us assume that $P(t)$ is the combination of two normal distributions, centered at T_1 and T_2 , each of them weighted by the corresponding probability of reinforcement, P_1 and P_2 . Subjects will normally start responding before T_1 and, if reinforcement does not arrive at this time, they will respond again around T_2 . What happens in between T_1 and T_2 ? Clearly, if T_1 and T_2 are similar to each other, subjects should not make a pause after T_1 . If, on the other hand, T_2 is much larger than T_1 , there will be a time in the trial when subjects are sufficiently sure that T_1 is past and T_2 still to come to cause a pause. Whether there is a pause or not, and how long the pause should be to maximize payoffs, must be determined for each specific experiment from the times and probabilities of reinforcement, the cost of responding, and the value of the reinforcer. The peak of response (average response time) generated by this conceptual model is plotted in Fig. 9 for different combinations of T_1 and T_2 , P_1 and P_2 , and β .

We can now apply these ideas to what should happen during a transition. Suppose that subjects react to the modification of reinforced time as if reinforcement might come at T_1 or T_2 with probabilities P_1 and P_2 , where P_1 decreases and P_2 increases as more and more trials are reinforced at T_2 (without any trial being reinforced at T_1 any longer). If subjects react like this to a modification of the time to reinforcement, Fig. 9 will describe the adjustment of peak time in an experiment

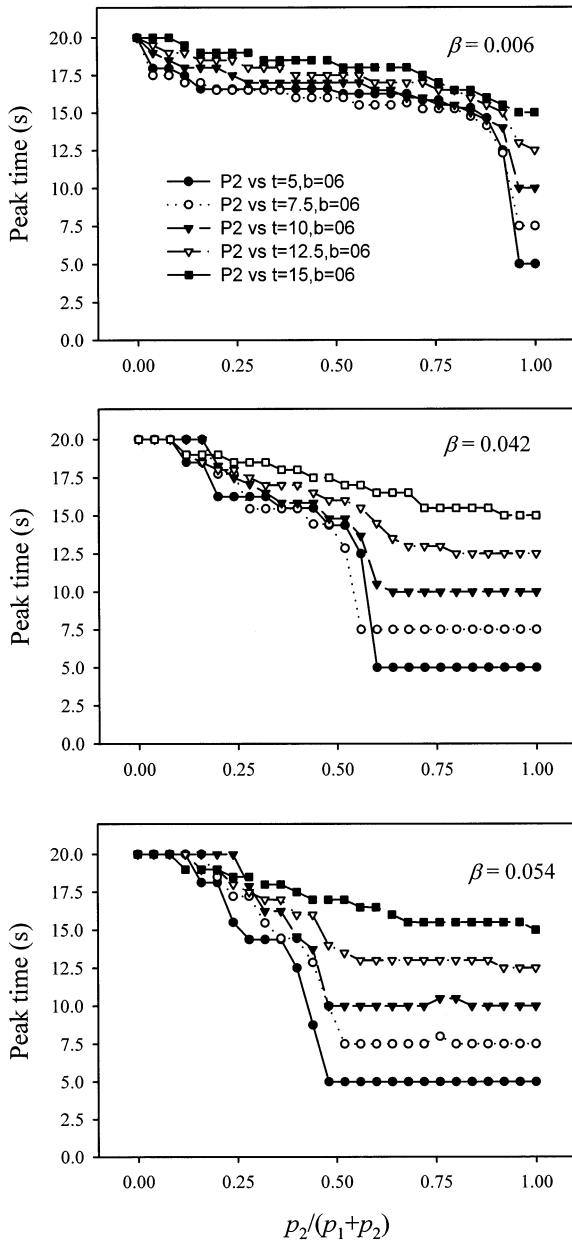


Fig. 9. Expected peak-response time (in s) when the expected probability of reinforcement is $P(t) = [P_1 \times P(t|T_1) + P_2 \times P(t|T_2)] / (P_1 + P_2)$ and starlings respond whenever $P(t) > \beta$. (Where $P(t; T_i)$ is a normal distribution with mean T_i and S.D. $0.2 \cdot T_i$). Each curve represents the value of the peak response time as a function of $P_2 / (P_1 + P_2)$. Within each panel, the five curves correspond to different values of T_2 ($T_1 = 20$ s in all cases), and the different panels are associated with different values of β (indicated in the upper, right-hand corner of the panels).

where the reinforced time changes from T_1 to T_2 : all we have to do is re-scale the x-axis so that it indicates trial number, instead of estimated value of P_2 .

Notice that, in Fig. 9, a number of adjustment patterns are shown: when T_1 and T_2 are close ($T_2 = 12.4$ and 15.0 s), the peak time changes gradually, regardless of the response threshold. When the two reinforced times are more easily discriminable ($T_2 \leq 10$ s), the transition is continuous for low threshold values (high response rates), proceeds roughly in two stages (which are not flat) for intermediate threshold values and, for very high thresholds, the intermediate stage shrinks to the extent that the pattern reminds of a one-step transition. It is clear from Fig. 9 that, when the adjustment proceeds in two stages, the intermediate stage does not lie around the geometric mean of the two times of reinforcement (as was the case in the results from Meck et al., 1984). The difference may simply come from the way in which peak time has been calculated: the method proposed by Meck et al. (1984) cannot be applied to our model, and different operational definitions of peak time (we used average time of the responding phase) can lead to quantitatively different results.

These considerations can help us understand the appearance of the steps as the overall probability of reinforcement decreases, a result first reported by Lejeune et al. (1997) and present also in our data. We have seen that the optimal response pattern will be dictated by cost-benefit trade-offs. If the response threshold increases as the probability of reinforcement decreases (as the probability of reinforcement decreases, responding becomes relatively more expensive), this increase in response threshold will be associated with the appearance of the two-stage transitions, as shown in Fig. 9.

Our approach can also shed light on the differences between the data on wait time and on the peak of responding. When subjects experience a transition from T_1 to T_2 , there is a stage during which both times have an above threshold probability of reinforcement, and subjects respond around both T_1 and T_2 . Hence, if $T_1 < T_2$, there is no reason to modify the time when responding

starts, as the start of responding is controlled by the memory for T_1 . On the other hand, if $T_1 > T_2$, subjects experience rewards earlier than before, and should start responding sooner because here wait time is controlled by T_2 . In other words, in downward transitions wait time should change immediately, but in upward transitions the modification should be more progressive, since delaying responding is only justified when the estimated probability of obtaining a reward at the earlier time is very low. This is the typical pattern of adjustment in wait times (Higa, 1997a,b). The difference between peak times and wait times stems from the fact that peak times are influenced both by the times to start and stop responding.

5. Implications for BeT and SET

The classical formulations of BeT and SET do not make specific predictions concerning what results should have been obtained in our experiments. BeT and SET represent two different philosophies of how is best to model behavioral timing. In SET (Gibbon, 1977; Gibbon and Church, 1984; Gibbon et al., 1984) the subject is modeled as measuring the length of relevant intervals with a clock, using working memory to hold the content of the clock as the interval elapses and finally storing the content of working memory in so-called reference memory, for later use. Behavior is generated by retrieving information from reference memory while measuring current elapsed time. Crucially, there is a decision subsystem that uses the stored information to generate actions, so that behavior does not reflect the unmodified content of memory (thresholds and comparison rules are involved). According to BeT (Killeen and Fetterman, 1988) the organism goes through a series of states, following a time-dependent sequence. Temporal regularities in the environment result in different states being associated with reinforcement, and appropriate behaviors re-occur when the animal finds itself in the reinforced state. No explicit representation of time intervals is proposed and no decision subsystem intervenes, other than the determination of the threshold above which an association between a

state and reinforcement is strong enough to respond. The timing of responses can vary if motivational factors speed up or slow down the rate of transition between states, if new states are associated with reinforcement, or if, for whatever reason, the strength of the association between a state and reinforcement required for responding changes.

Our qualitative model is easily translatable to the SET framework. SET assumes that the asymptotic representation in reference memory of the value of the time of reinforcement is a probability density function, with a maximum probability at the veridical interval length and spread proportional to this value. Todd and Kacelnik (1993) have proposed a memory-updating process that leads to a modification of reference memory which is very similar to the modification of the estimated probability of reinforcement, $P(t)$, described above (conceptually they are different: $P(t)$ includes other sources of uncertainty, such as that induced by time perception during the current trial). Hence, if the subject responds when the reference memory distribution is above a fixed threshold, all the considerations discussed for the optimality model apply.

A somewhat similar reasoning can explain how BeT might implement two-step transitions. If the length of the trials remains constant, as in the experiment reported by Meck et al. (1984), the rate of the pacemaker does not change and, therefore, the only way in which the subject can adapt to the new contingencies is by forming new associations between states of the animal and reinforcement (Killeen and Fetterman, 1988). We can imagine that the strength of the association between states and reinforcement changes in an analogous way to the memory representation of the time intervals in Todd and Kacelnik's 1993 model: in a reinforced trial, the association between the reinforced state and reinforcement increases, and the association between other states and reinforcement decreases. If subjects respond during those states that have an association with reinforcement greater than some fixed threshold, we find ourselves in the same scenario as before.

Both SET and BeT would seem to be compatible with the continuous and discontinuous ad-

justments reported in the literature. But this compatibility is achieved at a price. For instance, in order to make SET compatible with a two-step adjustment of the peak time, we have had to assume that subjects have some global knowledge of their reference memory contents (that is, that subjects ‘know’ $P(t)$ for all t : it is more frequent to assume that subjects do not have this knowledge, and that they behave on the basis of random samples—or some measure of the distribution central tendency—taken from reference memory at the beginning of each trial). If that were not the case in our situation we would not see the qualitative features described above, but neither would dual peak response patterns be obtained in multiple peak experiments such as

those reported by Bateson and Kacelnik (1997) and Leak and Gibbon (1995). Clearly, SET needs further refinements to accommodate both the properties of memory sampling and of expressions of differential responding at multiple temporal loci within each trial.

Likewise, although BeT can, in principle, be made compatible with a two-step adjustment to the new value of the reinforced time, we have been unable to simulate this result with the dynamic implementation of BeT recently proposed by Machado (1997). Machado’s model removes some of the flexibility inherent in BeT (as originally formulated by Killeen and Fetterman, 1988) by specifying two of its processes: credit assignment (how internal states are associated with ex-

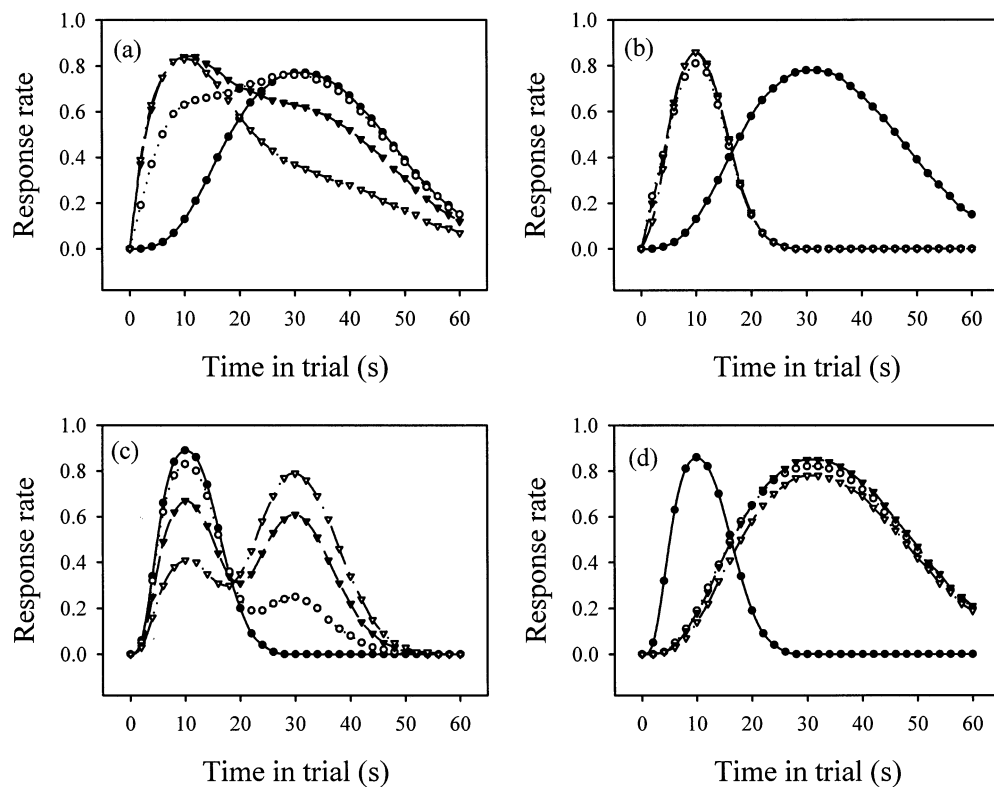


Fig. 10. Expected average response rate (arbitrary units), according to Machado’s (1997) model, as a function of time in the trial, before the transition (solid circles) and for several numbers of post-transition reinforced trials (empty circles: three trials, solid triangles: 12 trials, and empty triangles: 30 trials) when subjects experience a shift in the reinforced time from 30 to 10 s (a and b) or from 10 to 30 s (c and d). In (a) and (c) we assumed that the rate of the pacemaker, λ , remains constant after the transition. In (b) and (d), it approached the asymptotic value (calculated from the requirement that $\lambda \cdot T$ must be constant) exponentially, at the rate of 95% per trial at the new time to reinforcement.

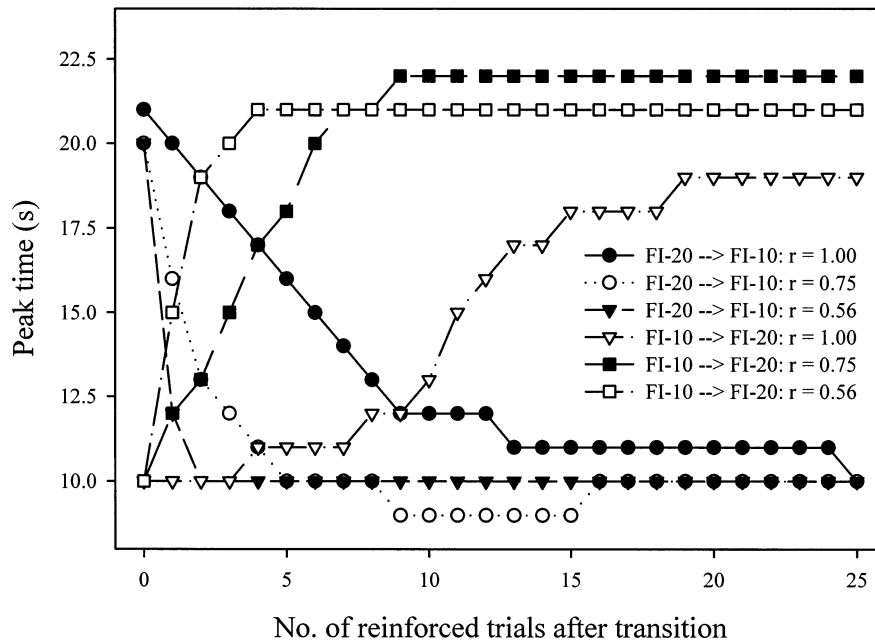


Fig. 11. Modification of the peak response time (s), according to Machado's (1997) model, as a function of the number of post-transition reinforced trials when subjects experience a shift in the reinforced time from 20 to 10 s (FI 20 \rightarrow FI 10) or from 10 to 20 s (FI 10 \rightarrow FI 20). For these simulations, we assumed that the rate of the pacemaker, λ , changes after each new post-transition reinforced trial according to the equation $\lambda' = \lambda_2 - r \cdot (\lambda_2 - \lambda)$, where λ is the rate of the pacemaker before the trial, λ' after the trial, and λ_2 its asymptotic value (calculated from the requirement that $\lambda \cdot T$ must be constant (Machado, 1997)). Different curves in the figure correspond to different values of r .

ternal events) and the relationship between strength of associations and behavior. Despite these restrictions, Machado's model retains four free parameters: two learning rate parameters, α and β (for asymptotic performance, only their ratio needs to be taken into account, but two values must be provided to study dynamics), the rate of the behavioral pacemaker, λ , and a motivational parameter, A (this one needs not to be taken into account when studying qualitative patterns). Moreover, the learning rate parameters take low values when fitting data from asymptotic performance and high values when fitting data from the dynamics of time discrimination (Machado, 1997), and the rate of the pacemaker must depend on reinforcement rate (as is the case with the original version of BeT, Killeen and Fetterman, 1988). These considerations imply that, when we try to fit data from a transition experiment as the one we have performed, some parameters (certainly λ) must be allowed to take different values

for different trials. In practice, this implies that Machado's model can account for a large number of transitional patterns (see Figs. 10 and 11 for some examples). And yet, we have been unable to find any set of parameter values leading to a two-step adjustment of peak rates (Fig. 10). In particular, changing the proportion of reinforced trial does not seem to have any effect on the pattern of adjustment. (Although we have tried a broad range of parameter values, not all values in this range have been used in our simulations. It is, of course, possible, that further investigation will show that some parameter values do exist which lead to a two-step transition.)

6. Concluding remarks

The results from experiments studying the dynamics of time discrimination showing both continuous and discontinuous transitions can be

accounted for using at least two theoretical approaches to timing, BeT and SET. We developed an argument based on maximization of the profitability of responding which shares important properties with SET (the time of expected reward is a probability density function that obeys Weber's Law). However, in our account it is not necessary to identify components such as working or reference memory, we simply assume that reward is expected at each time with a certain probability, that responding occurs when this probability is above some threshold and that in a transition changes of responding are due to gradual migration of response expectation between the original and the post-transition times. This smooth updating of estimated probability can generate several properties of the data, including discontinuities in some cases. We stopped short of developing a rigorous rate maximization model: this is perfectly possible using an equivalent to signal detection theory but testing such a model would require estimates of relative costs of responding to reward in order to derive an optimal value for the responding threshold and we have no such information at the moment. Hopefully, future experimentation will allow an even closer marriage of functional and mechanistic views of behavior in time-related tasks.

Acknowledgements

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Appendix A. Non-parametric test of continuity

This non-parametric test is based on the replicated goodness-of-fit test (Sokal and Rohlf, 1995). Consider first the data from a single subject: during the $N + 1$ trials following the transition, this subject has response peaks at times $t_0, t_1,$

$t_2 \dots, t_N$. These peak times can be decomposed as $t_i = \tau_i + \varepsilon_i$, where τ_i can be understood as the peak time in the absence of behavioral variance (whatever the sources of variance) and ε_i represents an error term, with unknown underlying distribution. In our experiment, we expect t_0 to be close to 20 s and t_N close to 10 s (assuming that behavior has stabilized by the N th trial).

In the absence of noise, if the transition between t_0 and t_N proceeded in k steps, the N differences $d_i = t_i - t_{i-1}$ would be as follows: k of them would be negative and the remaining ones would be equal to zero. In practice, even if the 'fundamental pattern' of the transition (as described by the τ_i) corresponds to k steps, the peak times will normally show fluctuations, and few of the d_i will be equal to zero. In this case, however, one would expect to find among the N differences: k negative and relatively large, the remaining randomly distributed, and adding up to zero (on average). In order to add up to zero, there should be about as many positive and negative values of the d_i (once the k large negative values have been removed) or, if there are more of one sign than of the other, those with the minority sign should have larger absolute values. With this in mind, it is easy to see how one would test the null hypothesis 'the underlying pattern of the transition has k steps':

1. Calculate d_i , for $i = 1, 2 \dots, N$.
2. Select the k largest negative values of the d_i (positive values if the steps are upwards).
3. If the underlying transition has more than k steps, among the remaining $N - k$ differences, there should be more negative than positive values and/or the negative differences should be larger (in absolute value) than the positive differences.

In all cases considered in this paper, the negative differences were, on average, larger (in absolute value) than the positive differences (although the difference was not significant). Therefore, if the number of negative differences was higher than the number of positive differences, one would have to conclude that the underlying transition proceeds in more than k steps ($k = 2$ for all the analysis presented in the paper). For a single subject, one could use a binomial test to compare the number of positive and negative differences.

For several subjects, one must use the replicated goodness-of-fit test (Sokal and Rohlf, 1995). This test is an extension of the binomial test which produces two statistics: G_h and G_p . G_h is associated with the homogeneity of the data from different subjects. If the data is homogeneous, G_h is approximately distributed as a χ_n^2 variate, where n is the number of subjects minus one. The statistic G_p is related to the hypothesis of interest: if the proportion of positive differences is equal to the hypothesized value P (in our case, $P = 0.5$), G_p follows a χ_1^2 distribution. Hence, all we need to do is to calculate G_p (Sokal and Rohlf, 1995) and look in a table for the probability that a variate with a χ_1^2 distribution yields this value. All P values given in the paper are two-tailed.

It is convenient to point out some caveats of this statistical test. First of all, since the test is based on the binomial test, it is not very powerful: large sample sizes are required to detect deviations from the null hypothesis. A more important problem is that, in practice, the test can be difficult to implement, for the following reason. Consider a subject which stabilizes its behavior after M trials, and suppose that this subject adjusts to the new environment in more than k steps. If the number of trials used for the test is $N < M$, it may be that the null hypothesis is not rejected simply because some of the steps have not been included in the analysis. Using a small number of trials for the analysis is therefore not desirable. If, on the other hand, $N > M$, the differences following the M th trial can be expected to be randomly distributed: as more trials are added (beyond the M th one), the overall proportion of negative differences approaches 0.5 even if there are more negative than positive differences among the initial M trials. Hence, one should not use more than M trials for the analysis either. The problem, therefore, is how to determine the value of M (the point when behavior stabilizes). In this paper, we have used visual inspection of the figures to determine the value of M (the same number of trials has been used for all subjects).

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