

Timing Competence and Timing Performance: A Cross-Species Approach

MARC RICHELLE^a AND HELGA LEJEUNE^b

Laboratory of Experimental Psychology
University of Liège
Liège, Belgium

INTRODUCTION

How animal behavior adjusts to or is shaped by time has been the central concern in at least two different scientific fields, fields that unfortunately have been kept separate until recently.¹⁻³ One is chronobiology, where the emphasis has been upon biological rhythms, as evidenced, at the behavioral level, by cyclic properties (circadian, circatidal, and the like) of spontaneous motor activity. The other field is experimental psychology, where the study of temporal regulations of behavior, initiated in Pavlov's laboratory, has received extensive treatment since operant techniques were developed. A wide variety of situations (schedules of reinforcement) are now available to investigate an animal's capacity to regulate its own behavior in time or to estimate the duration of external events. Refined analyses today combine the possibilities of conditioning procedures with sophisticated psychophysical models.⁴⁻¹⁴ This approach differs from the chronobiological tradition in two respects: First, it is mainly concerned with adjustment to arbitrarily chosen short durations (of the order of seconds or minutes), while chronobiology is concerned mainly, although not exclusively, with longer natural cycles. Second, chronobiology has been, from its earliest time, comparative and evolutionary, exploring a wide variety of species, plants and animals; while behavioral research on temporal regulation has been characterized by an almost total neglect of cross-species comparisons, which reflects the persistent belief that schedule-controlled behavior is essentially alike across animal species, including man.^{15,16} Data are obviously lacking to support such a general claim, and for what is known, it is clear that cross-species differences exist and should not be explained away.

Despite an increased interest in biological constraints on learning, very few systematic studies have been devoted to cross-species comparison of timing behavior and time estimation. Reviewing the literature 4 years ago, we could list only a dozen mammal species (besides the widely used rats and monkeys), half a dozen birds species (besides the much-favored pigeon), and half of a half-dozen of fish species; finally, bees were the only insect studied. Part of these studies are anecdotal, part bear only on one type of situation (fixed interval [FI] or differential reinforcement of low rates [DRL] in most cases), and part were carried out in our laboratory. Four more years have not added much to the record, which is in contrast with the expansion of research in more traditional laboratory species (rats and pigeons).

Other species investigated from 1979 include wood mice (*Apodemus sylvaticus* and *flavicolis*),¹⁷ turtle doves (*Streptopelia risoria*),¹⁸ fresh-water turtles (*Pseudemys*

scripta elegans),¹⁹ fish (*Tilapia nilotica* and *aurea*),²⁰ snakes (*Lampropeltis getulus floridana*),²¹ and fish crows (*Corvus ossifragus*).²²

The problems to be discussed in this paper will be illustrated with data from some of these studies. They are by no means sufficient to provide a clear picture of timing capacities throughout the animal kingdom or to make a choice among the various hypotheses that come to mind to account for cross-species differences. These admittedly speculative hypotheses have been formulated at length elsewhere.² They can be summarized as follows:

a. *The evolutionary hypothesis:* Temporal regulations of behavior become more refined and more efficient as we climb up the phyletic scale; briefly stated, they would parallel increased structural and functional complexity of the nervous system or increased potential for learning.

b. *The "egalitarian" or reductionist hypothesis:* The capacity for temporal regulations is equally distributed among all species—it would be as primitive and universal as biological rhythms are. In this view, observed differences would be nonessential, reflecting only inappropriate selection of responses, reinforcers, or situations by the experimenter.

c. *The ethological hypothesis:* Different species would exhibit different capacities for temporal regulations as a function of the particular repertoire evolved under selective pressure, similar demands being found at very different levels of the evolutionary scale. To make the point clear with a somewhat caricature-like example, predators might be thought of as having developed watching behavior—an advantage in temporal conditioning—while prey (at least those reacting to threat by running away) would not have developed such capacity.

Experimental strategies to be applied if one wishes to progress in the understanding of these problems are obvious, as are the difficulties involved. A first step, but it will be a long step, is to multiply the number of species studied, and to explore new species in different phylae of the zoological tree, which means bringing under experimental control wild species not used to living in the laboratory or in man's company. We cannot hope to study all created species, but we cannot dispense with the investigation of a reasonably diversified sample.

A second strategy consists in comparing species closely related on the phyletic scale. Will they exhibit similar performances or show differences, possibly more striking than those observed between more distant species?

A third strategy addresses a classical problem in cross-species study of behavior: Are we sure that the species compared are tested in equivalent situations? Has lever-pressing the same status for a rat, a cat, a monkey or a pigeon? What if we cannot bring a turtle to press with its paw? Will we use head-pushing as an equivalent unit of behavior? And still more puzzling for our concern: How can we know whether the delays and durations used are equivalent? Exploring various responses, reinforcers, or various ranges of delays in the same species is, of course, the only, if fastidious, way to answer such questions.

It is clear that data obtained using each of these three categories are to be interpreted in the light of data obtained with the others. The next sections provide illustrations of research with each strategy, kept apart for the sake of clarity.

I. COMPARING SPECIES AT VARIOUS LEVELS OF THE PHYLETIC SCALE

The experimental condition that has been most extensively used in exploring temporal regulations in various species is the fixed-interval (FI) schedule of reinforcement.

^a Address for correspondence: Université de Liège, Psychologie expérimentale, 5 boulevard du Rectorat (B32), Sart-Tilman, 4000 Liège, par Liège 1, Belgium.

^b Senior Research Fellow of the Fonds National de la Recherche Scientifique.

Under these contingencies, a reinforcement is delivered as a consequence of a subject's response, only after a fixed interval of time has elapsed since the last reinforced response. The periodicity of reinforcement entrains a regular alternation of postreinforcement pauses and operant activity, which is not the condition for reinforcement, but eventually develops spontaneously.

A dozen species have been submitted to FI schedules. Besides traditional laboratory or domestic animals such as rats, mice, cats, and pigeons, species less familiar to experimenters were tested, including turtledoves, wood mice, hapalemurs, tilapias and fresh-water turtles (more properly named terrapins²³). Conditioning new species raises in each case the problem of selecting an appropriate response (see section III later) and reinforcer. It also implies that the animal can adjust to the experimental situation. In some cases, for example, with hapalemurs and wood mice, subjects were living in seminatural conditions, with the conditioning chamber directly connected to their living quarters, so that they would present themselves spontaneously for the experimental sessions. These precautions do not solve all the problems involved in comparing performances under conditions that the experimenter might consider fairly similar, but that animals might view quite differently.

Behavior under FI schedules is amenable to analysis in terms of rate of responding or in terms of some index of temporal regulation. Rate of responding will be left out here, since it is known not to correlate with timing.²⁴ Among the various measures of temporal regulation that have been proposed (for a review of these see Richelle and Lejeune²), the curvature index (CI) of Fry *et al.*²⁵ has been used. It is computed from the distribution of responses in successive fractions of the interval, its maximal value being dependent on the number of subdivisions. Since the number of subdivisions was not always the same in different experiments, because of technical reasons, the value of the curvature index has been expressed as a ratio of the maximum value. Performances for those species in which curvature indices were available^c are shown in FIGURE 1. The interval values ranged from 20 sec to 10 min, but not all intervals were explored in all species.

Those species which rank highest are mammals, although not all mammals appear at the top. Cats, rats and mice (both laboratory mice and wood mice) show values around .70. Incidentally, the suggestion that the status of prey or predator might make a difference does not hold, at least in this particular experimental situation. Hapalemurs do not perform very well compared with other mammals: their curvature index ratio (CIR) is between .40 and .50. It might be that these very wild animals are not at their best in the experimental situation despite our efforts to make it as acceptable to them as possible. This might be the case also for the single representative of another prosimian species, *Perodicticus potto edwardsi*, which shows a very poor curvature index.

Second on our scale, right after mammals (with the reservations just formulated for prosimians), but with some overlapping, are birds—pigeons and turtledoves. Starlings, for which a curvature index is lacking, would plausibly join in the picture. Differences observed between pigeons and turtledoves will be discussed below.

Next come fishes (tilapias) and finally fresh-water turtles, which do not develop anything like the classical scalloping or break-and-run patterns of FI cumulative records.

As a first approximation, these comparative results suggest significant differences that might relate to the evolutionary status. The sample is, however, very limited and

^cFor a few species (golden hamsters, guinea pigs, starlings), tested with minimum technical facilities, only cumulative curves and total number of responses were available. They are not included here.

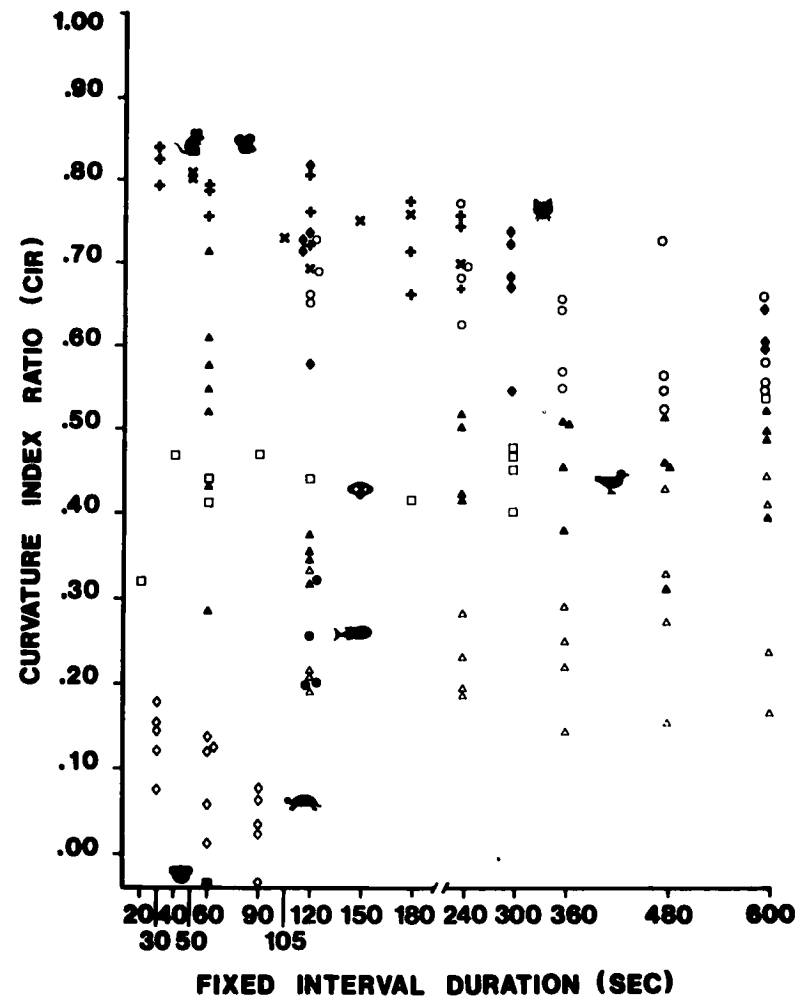


FIGURE 1. Curvature index ratio as a function of interval duration in fixed-interval schedule of reinforcement for individual subjects belonging to ten different species. Points plotted correspond to values averaged from a number of sessions of stabilized performance. Species are identified according to the following code: x = wood mice; + = laboratory mice (NMRI); ♦ = cats; O = rats; ▲ = pigeons; □ = hapalemurs; ● = tropical fish (tilapias); Δ = turtledoves; ◇ = freshwater turtles; ■ = *Perodicticus potto*.

fragmentary; nothing conclusive could reasonably be stated until many more species are tested. FIGURE 1 might suggest four qualitative levels, rather than a continuous progression, but at this stage such considerations are but speculative. Grouping of species, such as mammals at the upper level, might indeed result from the fact that the measure used leaves out more subtle differences in their respective competence for temporal regulations. The CIR values plotted on the graph were averaged from a number of successive sessions after behavior had "stabilized"—they correspond, it is hoped, to asymptotic behavior with respect to temporal regulation. It can be argued that this is exactly what we want to know. However, species might differ, not in their final adjustment to arbitrary (as opposed to natural) periodicities, but in the speed of

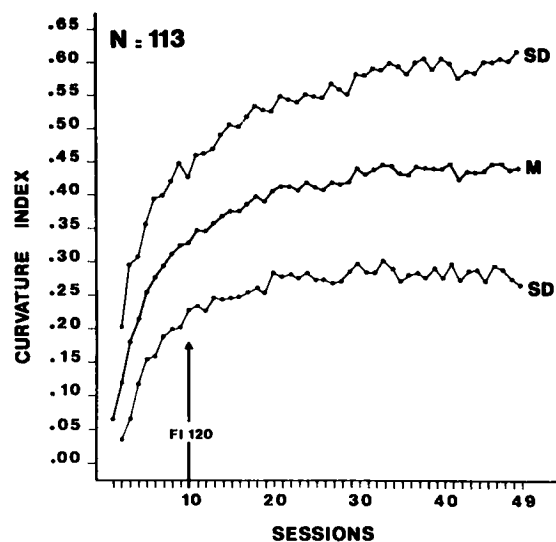


FIGURE 2. Evolution of the curvature index throughout training under fixed-interval schedule of reinforcement in rats. Results plotted are averaged from 113 animals. The interval was brought to 120 sec after 10 sessions. Because it is computed from a partition of the interval into four segments, the curvature index can take a maximal value of .75. The line in the middle represents the means; the lines above and below represent the standard deviations.

acquisition. Cross-species performances should be compared, for instance, in terms of the number of sessions to stabilized behavior. Given within-species interindividual differences, that type of comparison would require larger samples of subjects than are usually available in experiments that extend over several months. An exceptionally large sample of rats has been studied by one of us.²⁶ FIGURE 2 shows the average "acquisition curve" from 113 subjects run on FI 120 sec. After progressive increase of the interval to its final value over 10 sessions, it took about 20 sessions on 120 sec to reach stabilization (that is, asymptotic behavior).

Interindividual differences deserve further attention. Frequently noted by experimenters in temporal schedules, these differences have not prompted systematic

inquiries into the variables responsible for them. While the mean CI remained fairly constant from the 29th session on, the standard deviation increased throughout sessions 20 to 49. Thus, individual differences rather than leveling out became more marked as learning progressed. Rank correlations (Kendall's *tau*) computed between adjacent sessions, and between early sessions and later sessions were in the range of .30 to .50 (statistically significant at $p \leq .001$). This indicates that subjects who ranked high in CI early in training tended to remain good, and vice versa. These data encourage a behavioral genetics approach, with classical problems of chronobiology in mind, that is, the genetic aspects of biological (and for that matter, behavioral) clock(s). However, before starting a systematic selection of good and bad "temporal regulators," the behavioral scientist first must make decisions as to the criteria to be used in such categorizing and as to the relevant schedule. Things would be easy if subjects ranked similarly in different experimental conditions, so that, for instance, FI performances correlated with DRL performances, or with discrimination of response duration, and so forth. Preliminary results comparing FI and DRL in the same subjects showed that this is not the case, so that one has to make an arbitrary choice. Moreover, order effects are important. For example, FI performances are much influenced by previous exposure to DRL schedules.²⁷

The schedule of differential reinforcement of low rates (DRL) is, after FI, the most widely investigated experimental situation. Temporal regulation is, in DRL, the condition for reinforcement. An often-noted paradox, which remains to be elucidated, is that animals who pause spontaneously after FI reinforcement for periods of one or several minutes seem unable to refrain from responding for delays beyond a few seconds in DRL. This has been repeatedly described for pigeons, using the traditional key-peck response. While pigeons would pause for more than 1 minute in FI 120 sec (and longer in FI with longer intervals), they do not adjust efficiently to DRL beyond 12 or 15 sec, showing a IRT median value farther and farther away from the critical reinforced value.^{28,29} The same relation holds, if sometimes less dramatically, for other species submitted until now to DRL schedules.

FIGURE 3 shows individual results in DRL (5 to 60 sec) for different species studied in our laboratory. They are fewer in number than for the FI schedule, because it is both logical and technically easier to start with FI.

Incomplete as it is, the picture is no less complicated than for FI. Mammals rank highest, with cats and rats first, together with wild mice. Hapalemurs are slightly below, but are clearly higher than birds. Laboratory mice perform poorly. Subjects from three different strains (NMR1, C57BL/6J and Balb/c) have median IRTs ranging from 5.6 to 18.8 sec for critical delays of 20 sec. This is in contrast with their wild brothers, whose median IRTs match the critical value up to 20 sec (and up to 30 sec for one individual).

Pigeons and turtledoves perform poorly, with pigeons slightly better, as in FI schedule.

In interpreting these results, one should take into account the fact that the longest delay explored was dictated by the limits of performance observed in a given species. Exploring values beyond 10 to 15 sec in pigeons, turtledoves or laboratory mice was revealed to be useless.

Median IRT is only one of several possible ways of characterizing timing performance under DRL contingencies. It recommends itself as a practical, simple and plausibly valid index, useful at this still crude stage of cross-species comparisons. It might very well be that more refined statistics will be needed when more subtle differences between species will have to be examined. Dispersion of IRT distribution, for instance, might reveal a more discriminative tool.

The same remark just formulated about the use of stabilized performance under FI

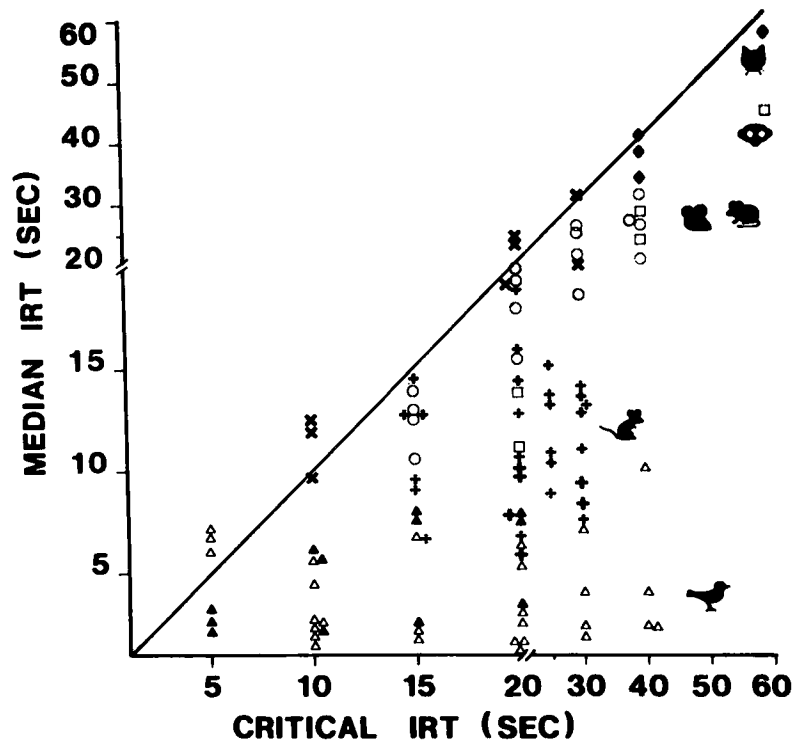


FIGURE 3. Median interresponse time (IRT) as a function of the critical delay in a schedule of differential reinforcement of low rates (DRL) in individual subjects belonging to seven different species. The diagonal line corresponds to a perfect match of median IRT with the critical delay. Results plotted correspond to values averaged from a number of sessions of stabilized behavior. Species are identified according to the following code: x = wood mice; + = Balb/c mice; + = NMR1 mice; + = C57BL/6J laboratory mice; ♦ = cats; O = rats; ▲ = pigeons; Δ = turtledoves; □ = hapalemurs.

schedules holds true for DRL: Species might differ in their speed of acquisition—length of exposure to contingencies needed to reach asymptotic performance—rather than in their stabilized temporal regulation.

Comparing the results summarized in FIGURES 1 and 3 suggests a few additional comments.

The position of hapalemurs in contrast with birds (pigeons and turtledoves) is very different in FI and DRL: Our prosimians generally performed less well than birds in FI, while they seem much better integrated among the mammal group under DRL. However, one should not speculate about these differences until one considers the issues discussed in section III.

More interesting is the evolution of temporal regulation of behavior as a function of interval or delay under FI and under DRL. In the first case, the CIR sometimes

increases (improved performance), sometimes decreases (impaired performance), or remains unchanged, depending upon the species and/or the individual. Of course, the observed trends should not be extrapolated to longer intervals. However, it is worth noting that performance (in terms of CIR) sometimes improves as the interval increases within the limited range of intervals explored.

Nothing similar is observed under DRL. At best, performance comes close to the diagonal line of the median IRT/critical delay plot, up to a certain delay, and then it drifts away more or less abruptly. This might reflect an important difference between what we have called *spontaneous* temporal regulation of behavior versus *required* temporal regulation.²

II. COMPARING CLOSELY RELATED SPECIES

Before drawing any tentative conclusion from the cross-species comparison, we must take a closer look at the differences between the two pairs of closely related species that have been deliberately introduced in our studies.

A first observation is that closely related species may rank differently in different situations. Laboratory mice and wild mice perform similarly under FI, but the former are distinctly below the latter in DRL. That the difference goes in that direction is altogether intriguing and reassuring—intriguing because one would somewhat anthropomorphically expect that laboratory animals would be better prepared to laboratory situations, and reassuring because this indicates that our efforts to make the experimental situation acceptable to wild animals have been fairly successful.

Secondly, although they are drawn from two situations only, these data indicate that it would be unadvisable to characterize timing competence from behavior observed in one single situation. Which of FI or DRL (and of many other conditions one might wish to explore) is the best indicator of such competence is, of course, undecidable.

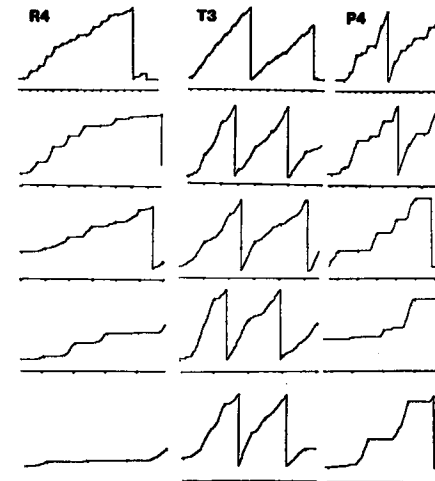


FIGURE 4. Typical cumulative records from one turtledove (T3), one pigeon (P4), and one rat (R4) trained under a fixed-interval schedule, with interval values (top to bottom) of 2, 4, 6, 8 and 10 minutes. Availability of reinforcement is signaled by deflection of the pen tracing the horizontal line under the cumulative curve. The cumulative pen sets back after 360 responses.

Under FI contingencies, pigeons differ from turtledoves both in rate of responding (which is higher in turtledoves) and in curvature index (higher in pigeons). Details of the comparison between the two species, and between each of them and rats, for FI delays from 2 to 10 min can be found elsewhere.³⁰ Subjects in this experiment experienced long exposures (30 to 40 sessions) to each value of the interval. Turtledoves did not exhibit, except occasionally, the typical postreinforcement pause, which has usually been taken as a universal pattern, as can be seen from the cumulative records in FIGURE 4. It had been observed previously that this pattern was not as marked in pigeons as it is in rats.³¹ Its almost total absence in turtledoves' behavior is all the more striking since they are zoologically close to pigeons and since a response of identical topography was used.

These comparisons between closely related species throw some doubt on the plausibility of the eco-ethologic hypothesis: How can we account for these differences in terms of differences in selective pressure? We throw out this challenge to our ethologist colleagues.

This comparison also throws some doubt on the evolutionary hypothesis, at least if we want to give it a refined form and are not satisfied with a crude three or four-level scale. Differences between cats and pigeons should not be given too much weight if differences almost as large are observed between pigeons and turtledoves.

III. COMPARING RESPONSES WITHIN SPECIES

Before speculating on the position of a species on an ideal timing competence scale, one should ask another critical question: Are the experimental conditions adequate to reveal the real competence of our subjects? Just as psychologists studying intelligence years ago asked whether IQ tests are culture-free or culture-fair tests, so too have behavioral scientists been questioning for some 10 or 15 years the validity of the selected responses or stimuli. (Credit should be given, however, to a few early pioneers; see Bitterman.³²) The early belief in the arbitrariness of operant responses (with its corollary: the assumed cross-species equivalence of similar or even nonsimilar motor units) has been shaken under the influence of ethology after a number of experimental findings drew the attention of experimenters to what is now familiar under the label *biological constraints on learning, or species-specific status of response or stimuli*.³³⁻³⁷ Pigeons' key-pecks have been submitted to special scrutiny in this respect. The status of that particular response in the natural food-searching and eating repertoire of the species and the fact that it is amenable to Pavlovian conditioning (as seen in the famous autoshaping paradigm^{38,39}) have led us to wonder whether the legendary mediocrity of pigeons under DRL might not be response-bound. It is well known that IRT distributions are biased by the presence of response bursts that load the shortest IRT class, and that these particular responses, usually of extremely brief duration themselves, are not amenable to contingency control.^{40,41} These responses are observed in FI schedules as well and their presence in the first part of the interval accounts for part of interindividual variability in CI. Data from pigeons in FI 60 sec plotted in FIGURE 5 have been treated both ways: including and excluding responses occurring in the first tenth part of the interval. It is clear that the second procedure considerably reduces variability.

Several investigators have resorted to a response less involved in the alimentary behavior of pigeons, that is, treadle-pressing.⁴² Using this response, pigeons perform better in DRL than they do with key-pecking. Lejeune and Jasselette⁴³ have compared treadle-pressing and key-pecking in the same individual subjects, both in FI and in

fixed-time (FT) schedules—an equivalent of Pavlov's periodic conditioning, where the grain reinforcement is presented at regular intervals independently of the subject's behavior. Subjects were trained to press a treadle under FI 60 sec for 90 sessions, then under FT 60 sec for 35 sessions, and were exposed to FI 60 again for 20 sessions. Then they were submitted to a similar program with key-pecking. Their data confirm previous results⁴⁴ showing that response rate is higher for key-pecking than for treadle-pressing. There is, however, no significant difference between CI values for the two responses, whether or not responses in the first segment are taken into account for computation. Suppression of response-reinforcement contingencies (FT schedule) reduces overall response output, but does not significantly affect temporal regulation, until responding eventually is extinguished. This is true, in this experiment, for key-pecking as well as for treadle-pressing contrary to other authors' findings³¹

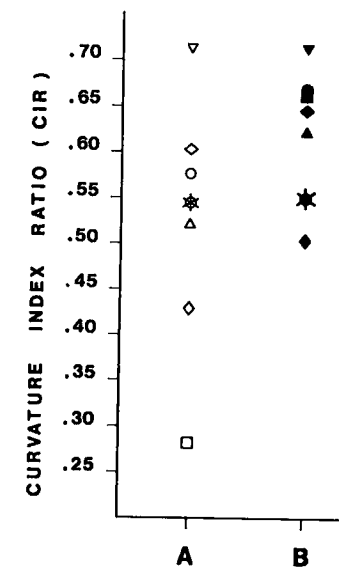


FIGURE 5. Values of the curvature index ratio obtained in pigeons when responses emitted in the first tenth of the interval are included or left out for computation. Individual results computed from the last ten sessions of a 90-session run under fixed interval 60 sec. Left (A, open symbols): first segment responses included; right (B, solid symbols): first segment responses left out.

showing that key-peck responses are maintained at high levels under FT 60. When FI contingencies are reinstated, the key-pecking response rate quickly returns to previous FI level while the treadle-pressing rate remains much lower.

The idea of training pigeons to press a treadle with their foot is, obviously, an unimaginative transfer on the part of experimenters used to train rats to lever press. In most persons' eyes—not only in ethologists'—this might appear as a strange and difficult movement for those birds. Looking for a more natural operant, plausibly more appropriate to reveal timing competence in birds, we designed an experimental situation where perching was the response. Pigeons, and later turtledoves, were trained to jump on a perch and sit on it for a minimal period of time (defined as the *critical response duration*) in order to have access to grain. This schedule is more appropriately labeled *differential reinforcement of response duration* (DRRD) rather than DRL. Keep in mind that pigeons do not succeed in spacing their key-pecks to match

critical delays longer than 12 or 15 sec or so in DRL. Subjects were trained both in DRRD (perching) and in DRL (key-pecking). Critical delays in DRRD were 10, 20, 30, 40, 50 sec; they were 5, 10, 15 and 20 sec in DRL (exploring longer delays was meaningless, since performance was already very poor at these values). Details of the procedures and results for pigeons can be found in Lejeune and Richelle.⁴⁵ Results obtained with turtledoves are still unpublished. Main findings for both species are plotted in FIGURE 6, showing median response durations and median IRTs for individual subjects as a function of *critical response duration* and of critical DRL delay, respectively. Both species are able to estimate duration of their own perching behavior much better than they are able to control IRTs in key-pecking DRL. Median response duration for pigeons is very close to the critical value up to 40 or 50 sec. Turtledoves compare with pigeons up to 20 sec; beyond that value they fall a bit lower, except for one individual subject that ranks first at 50 sec. Relative frequency distributions of response duration clearly reflect the quality of temporal regulation as contrasted with IRT distribution in DRL. FIGURE 7 shows a typical individual example for both responses in the two species.

In both species, the symmetric distributions of perching durations, with a mode close to the critical value, contrast with asymmetry of IRT distributions, whether or not the first time bin is taken into account.

One might argue that the two situations differ in other respects than the response used. For instance, in the perching situation, the subject initiates a trial by jumping on the perch, while in classical DRL (that is, in our key-pecking situation) a key-peck altogether terminates the "trial" (IRT) and initiates the next one, making the time estimation task a continuous one. Consuming the reinforcer is always part of the

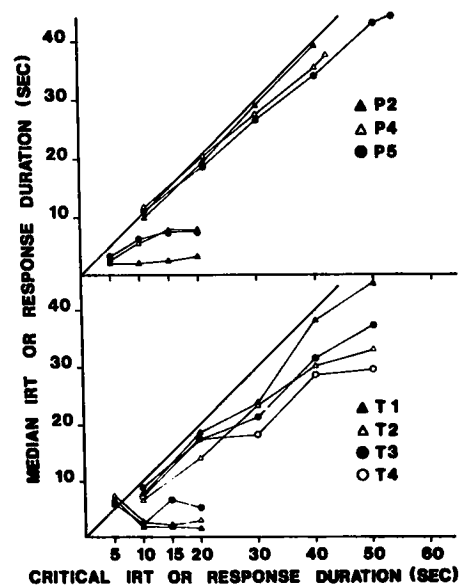


FIGURE 6. Comparison in pigeons and in turtledoves between performance under DRL schedule/key-pecking response and performance under a schedule of differential reinforcement of response duration (DRRD)/perching response. Ordinate: median IRT (for DRL/pecking) or response duration. Abscissa: critical delay or response duration. Top: pigeons (P); bottom: turtledoves (T). Individual data were averaged from a number of sessions of stabilized behavior.

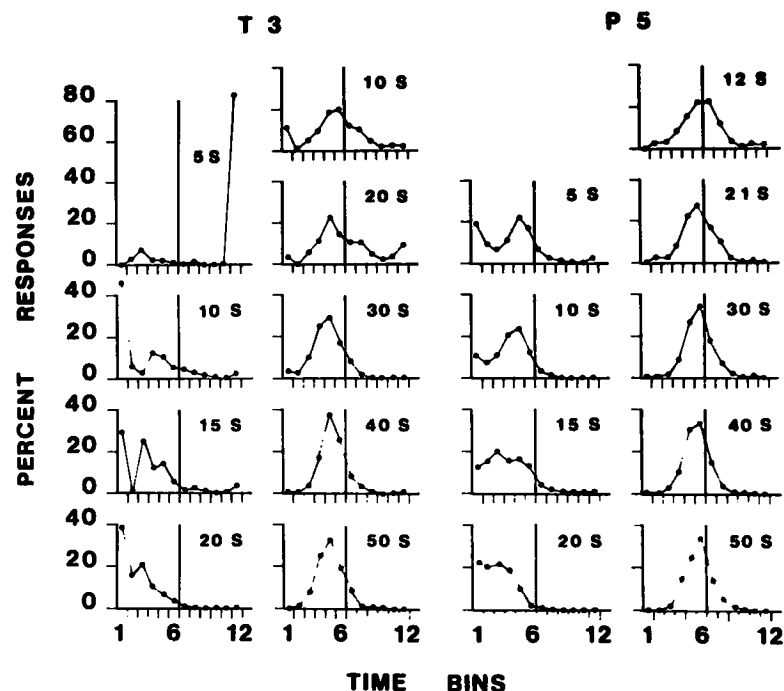


FIGURE 7. Relative frequency distribution of IRTs and of response durations obtained under DRL/key-pecking and DRRD/perching schedules, respectively, for increasing values of the critical delay or duration (top to bottom). Data presented are for two typical individuals: one pigeon (right columns) and one turtledove (left columns). Each time bin on the abscissa is equal to one-sixth of the critical delay or duration. IRTs or response durations falling in the seventh bin or above (that is, right of the vertical fine line) were reinforced. Note that the critical perching duration has been extended up to 50 sec with excellent performance, while with key-pecking, critical delays beyond 20 sec were not judged worth exploring.

postreinforcement IRTs in DRL, while it is not included in response duration in perching DRRD. These differences might be easily eliminated by slight modifications in procedures (see Lejeune and Richelle⁴⁵ for suggestions). These differences, however, are not crucial for our present concern. Whatever the variables accounting for contrasting performances in the two situations, it is clear that using another response and a slightly different schedule reveals in birds a timing competence that went unsuspected when the most popular operant behavior was used.

DISCUSSION

Experimental data presented in this paper illustrate the extreme intricacies of any attempt to build a coherent cross-species characterization of temporal regulation of behavior. They indicate how difficult it is to appraise the very competence of various

animal species in adjusting their own behavior to arbitrary durations as defined by experimenters. It might very well be that this competence is indeed inaccessible, or even uninferable, or that no such thing exists at all. Performances would be the only things to look at, and all that could be compared, at best, would be the best performances obtained in each species studied.

This implies that experimenters not only explore various species, but look for "species-fair" tests that reveal the best of each species' timing capacities. In the examples above, the nature of the response has been emphasized. The response has been, no doubt, the privileged variable in the recent awareness-raising movement concerning species-specific constraints among conditioning psychologists. Stimuli and reinforcers deserve similar attention.

The use of alimentary reinforcers (food or water) raises a number of problems when the experimenter deals with species whose eating and drinking habits are simply not known or are not as familiar to him or her as those of traditional laboratory animals. An ethological description of alimentary behaviors and a physiological study of metabolic processes typical of a species are prerequisites before any interpretation of the performances observed can be seriously proposed, especially when performances show limitations. In view of the poor performance obtained from turtles in our laboratory, and of the failure to obtain in snakes anything like the classical FI "scallops," as reported earlier by Kleinginna and Currie,²⁰ it is tempting to conclude that reptiles are poor "timers." Besides the fact that two species can hardly be taken as representative of a whole zoological class, one should ask whether daily sessions with intermittent food or water reinforcers, using arbitrarily selected delays (usually after the experimenter's habit with rodents or birds) are really adequate conditions to test timing capacities in these organisms.

In the particular case of temporal regulations of behavior, which are our concern here, it would seem essential to pay special attention to species-specific constraints on the delay variable. Such constraints might be thought of as bound to the natural temporal spacing of feeding behavior, as just mentioned above, but also to the rhythm of motor activity, the sleep cycles, sexual cycles, and the like. Rather than using arbitrary delays, intervals, or stimulus durations, experimenters should take into account species-specific biological cycles and match their temporal parameters to natural periodicities as experienced or exhibited by the organism under study. There are some, unfortunately few, indications that species such as bees can be trained to forage for food at specific intervals of time approximating their circadian cycle, which is in contrast to the absence of conditioned periodicity when they are exposed to FI contingencies up to 90 sec.^{46,48} The interactions and interdependencies between "natural" biological rhythms, as studied in the field of chronobiology, and temporal regulations of behavior, as analyzed in the laboratory by psychologists, offer a fascinating area of research, still almost totally unexplored. Such an integrated approach is the condition for testing some of the hypotheses that come to mind concerning the timing competence of various animal species. One hypothesis we would favor for future research might be phrased as an adapted version of Kurt Richter's view: Through biological evolution, species would exhibit increased capacities to free themselves—when useful for survival in some way—from basic biological periodicities and to adjust to "arbitrary" delays or durations, that is, delays without relation to biological rhythms.

REFERENCES

1. RICHELLE, M. 1968. Notions modernes de rythmes biologiques et régulations temporelles acquises. In *Cycles Biologiques et Psychiatrie* J. de Ajuriaguerra, Ed.: 233-255. Georg et Cie, Genève; Masson, Paris.

2. RICHELLE, M. & H. LEJEUNE. 1980. Time in Animal Behaviour. Pergamon Press. Oxford.
3. ELSMORE, T. F. & S. R. HURSH. 1982. Circadian rhythms in operant behavior of animals under laboratory conditions. In *Rhythmic Aspects of Behavior*, F. M. Brown & R. C. Graeber, Eds.: 273-310. Lawrence Erlbaum Associates.
4. GIBBON, J. 1977. Scalar expectancy theory and Weber's law in animal timing. *Psychol. Rev.* 84: 279-325.
5. GIBBON, J. 1979. Timing the stimulus and the response in aversive control. In *Advances in Analysis of Behaviour* (Vol. 1): Reinforcement and the Organization of Behaviour. M. D. Zeiler & P. Harzem, Eds. Wiley. Chichester and New York.
6. GIBBON, J. & R. M. CHURCH. 1981. Time left: Linear versus logarithmic subjective time. *J. Exp. Psychol. Anim. Behav. Processes* 7: 87-108.
7. PLATT, J. R. 1979. Temporal differentiation and the psychophysics of time. In *Advances in Analysis of Behaviour* (Vol. 1): Reinforcement and the Organization of Behaviour. M. D. Zeiler & P. Harzem, Eds. Wiley. Chichester and New York.
8. ZEILER, M. D., E. R. DAVIS & A. J. DE CASPER. 1980. Psychophysics of key-peck duration in the pigeon. *J. Exp. Anal. Behav.* 34: 23-33.
9. ROBERTS, S. 1981. Isolation of an internal clock. *J. Exp. Psychol. Anim. Behav. Processes* 7: 242-268.
10. ROBERTS, S. 1982. Cross-modal use of an internal clock. *J. Exp. Psychol. Anim. Behav. Processes* 8: 2-22.
11. MECK, W. H. & R. M. CHURCH. 1982. Abstraction of temporal attributes. *J. Exp. Psychol. Anim. Behav. Processes* 8: 226-243.
12. STUBBS, D. A. 1980. Temporal discrimination and a free-operant psychophysical procedure. *J. Exp. Anal. Behav.* 33: 167-185.
13. CHURCH, R. M. & J. GIBBON. 1982. Temporal generalization. *J. Exp. Psychol. Anim. Behav. Processes* 8: 165-186.
14. PLATT, J. R. & E. R. DAVIS. 1983. Bisection of temporal intervals by pigeons. *J. Exp. Psychol. Anim. Behav. Processes* 9: 160-170.
15. SKINNER, B. F. 1965. A case history in scientific method. *Am. Psychol.* 11: 221-233.
16. LOWE, C. F. 1983. Radical behaviorism and human psychology. In *Animal Models of Human Behavior*. G. C. L. Davey, Ed. J. Wiley, New York, NY.
17. LEJEUNE A. & H. LEJEUNE. 1983. Fixed interval and differential reinforcement of low rate performances in wood mice (*Apodemus sylvaticus and flavicollis*). Unpublished report. Laboratory of Experimental Psychology, University of Liège.
18. LEJEUNE, H. 1983. Differential reinforcement of perching duration in the turtle dove: A comparison with differential-reinforcement-of-low-rate key-pecking. Unpublished report, Laboratory of Experimental Psychology, University of Liège.
19. LAURENT, E. 1983. Régulation temporelle acquise chez la tortue semi-aquatique *Pseudemys scripta elegans* (Wied). Unpublished Master's thesis, University of Liège.
20. GRAILET, J. M., JEANGILLE, L., MICHAUX, L., QUEVRIN, A., LEJEUNE, A. & H. LEJEUNE. 1981. Etude de la régulation temporelle en FI 120 chez les *Tilapia nilotica et aurea*. Unpublished report, Laboratory of Experimental Psychology, University of Liège.
21. KLEINGINNA, P. R. & J. A. CURRIE. 1979. Effects of intermittent reinforcement in the Florida kingsnake (*Lampropeltis getulus floridana*). *J. Biol. Psychol.* 21: 14-16.
22. POWELL, R. W. & W. A. KELLY. 1979. Crows learn not to respond under response-independent reinforcement. *Bull. Psychonom. Soc.* 13: 397-400.
23. CAGLE, F. R. & A. H. CHANEY. 1950. Turtle population in Louisiana. *Am. Midl. Nat.* 43: 383-388.
24. DUKICH, T. D. & A. E. LEE. 1973. A comparison of measures of responding under fixed-interval schedules. *J. Exp. Anal. Behav.* 20: 281-290.
25. FRY, W., R. T. KELLEHER & L. COOK. 1960. A mathematical index of performance on fixed-interval schedule of reinforcement. *J. Exp. Anal. Behav.* 3: 193-199.
26. LEJEUNE, H. 1983. Inter-individual differences in FI performance in rats: A large group study (N = 113). Unpublished report, Laboratory of Experimental Psychology, University of Liège.
27. FRANSOLET, R. 1981. Contribution à l'étude des régulations temporelles FI et DRL chez le rat. Unpublished Master's thesis, University of Liège.
28. DEWS, P. B. 1970. The theory of fixed-interval responding. In *The Theory of Reinforcement Schedules*. W. N. Schoenfeld, Ed.: 43-62. Appleton-Century-Crofts. New York, NY.

29. STADDON, J. E. R. 1965. Some properties of spaced responding in pigeons. *J. Exp. Anal. Behav.* 8: 19-27.
30. LEJEUNE, H. & M. RICHELLE. 1982. Fixed interval performance in turtle doves: A comparison with pigeons and rats. *Behav. Anal. Lett.* 2: 87-95.
31. LOWE, F. & P. HARZEM. 1977. Species differences in temporal regulation of behavior. *J. Exp. Anal. Behav.* 28: 189-201.
32. BITTERMAN, M. E. 1975. The comparative analysis of learning. *Science* 188: 699-709.
33. BRELAND, K. & M. BRELAND. 1961. The misbehavior of organisms. *Am. Psychol.* 16: 661-664.
34. SHETTLEWORTH, S. J. 1972. Constraints on learning. *In Advances in the Study of Behavior*, Vol. 4. D. S. Lehrman, R. A. Hinde & E. Shaw, Eds.:1-68. Academic Press. New York, NY.
35. HINDE, R. A. & J. STEVENSON-HINDE. 1973. Constraints on Learning. Academic Press. London and New York.
36. SELIGMAN, M. E. P. & J. L. HAGER, Eds. 1972. Biological Boundaries of Learning. Appleton-Century-Crofts. New York, NY.
37. SCHWARTZ, B. 1978. Psychology of Learning and Motivation. W. W. Norton. New York, NY.
38. BROWN, P. L. & H. M. JENKINS. 1968. Auto-shaping of the pigeon's keypeck. *J. Exp. Anal. Behav.* 11: 1-8.
39. LOCURTO, C. M., H. S. TERRACE & J. GIBBON, Eds. 1981. Autoshaping and Conditioning Theory. Academic Press. New York, NY.
40. BLOUGH, D. S. 1966. Reinforcement of least-frequent interresponse times. *J. Exp. Anal. Behav.* 1966. 9: 581-591.
41. MILLENSON, J. R. 1966. Probability of response and probability of reinforcement in a response-defined analogue of an interval schedule. *J. Exp. Anal. Behav.* 9: 87-94.
42. HEMMES, N. S. 1975. Pigeon's performances under differential reinforcement of low rate schedule depends upon the operant. *Learn. Motiv.* 6: 344-357.
43. LEJEUNE, H. & P. JASSELETTE. 1983. Fixed interval and fixed time treadle pressing in the pigeon: A comparison with FI and FT keypecking in the same subjects. Unpublished report, Laboratory of Experimental Psychology, University of Liège.
44. RICHARDSON, W. K. & N. RAINWATER. 1979. A comparison of the keypeck and treadlepress operants in the pigeon: Fixed interval schedule of reinforcement. *Bull. Psychon. Soc.* 14: 333-336.
45. LEJEUNE, H. & M. RICHELLE. 1982. Differential reinforcement of perching duration in the pigeon: A comparison with differential-reinforcement-of-low-rate keypecking. *Behav. Anal. Lett.* 2: 49-57.
46. BELING, I. 1929. *Z. Vgl. Physiol.* 9: 259-338.
47. GROSSMAN, K. E. 1973. Continuous, fixed-ratio and fixed-interval reinforcement in honey bees. *J. Exp. Anal. Behav.* 20: 105-109.
48. PALMER, J. D. 1976. *An Introduction to Biological Rhythms*. Academic Press. New York and San Francisco.

The Integration of Reinforcements over Time

S. E. G. LEA^a

*Department of Psychology
University of Exeter
Exeter, England*

S. M. DOW

*Department of Zoology
University of Bristol
Bristol, England*

INTEGRATION OVER TIME: A NEGLECTED PROBLEM

The title of this paper could as well have been "The Integration of Prey over Time." We are concerned with a problem that is common to the experimental analysis of animal behavior as it occurs in Skinner boxes, and to the empirical investigation of foraging as it occurs in the animal's natural environment. It is the problem of how a series of discrete events, deliveries of reinforcers or captures of prey, are transformed into an estimate of the density of reinforcements available on a schedule, or the density of prey present in a patch.

All popular accounts both of foraging behavior and of behavior under schedules of reinforcement make use of the results of such an integration. Herrnstein's^{1,2} matching law and "quantitative law of effect" predict that behavior under schedules of reinforcement will be a function of the reinforcement rates experienced under the schedules. Charnov's³ marginal value theorem predicts that natural foraging behavior in a patchy environment will be a function of the rates at which prey can be captured within each patch and within the environment as a whole. The functions concerned are different, but the problem is common to both.

You or I, faced with the problem of estimating the rate at which discrete events occur, would doubtless solve it by counting them, then dividing by the time that had elapsed, or the number of responses we had made. We have no evidence that animals can use this solution. So far as we can tell, the capacities of even the largest-brained birds to discriminate between numbers are quite modest.⁴ (Other kinds of "counting" behavior, which appear to be much more accurate,^{5,6} turn out to be no different from the kind of noncounting mechanism we propose below.) We have no evidence at all that animals can manipulate numbers in the kind of way required for division. Besides, this solution ignores an additional, fundamental aspect of the problem: the density that is being estimated is liable to change.

In the laboratory we do, of course, change the schedules of reinforcement that our subjects experience. But, except in the case of the transition to extinction, we very rarely study the effects of these transitions. Instead, we maintain the same conditions in force until we are sure we have achieved "steady-state" behavior, and look only at

^aAddress for correspondence: S. E. G. Lea, University of Exeter, Department of Psychology, Washington Singer Laboratories, Exeter EX4 4QG, England.