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Chapter 5. From Biotemporality to Nootemporality: Toward an Integrative and Comparative View of Time in Behavior¹

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The title of this paper refers to the levels of temporality as proposed by J.T. Fraser (1982) and, more precisely, to the two highest levels on a scale of cosmic evolution. Whatever the epistemological status of Fraser's levels concept (for a thoughtful discussion see Michon, 1985c, also chapter 20 of the present volume), it is obvious that time in living systems on the one hand and time in human and infrahuman behavior and mind on the other appear as two distinct fields of research. Roughly, the first is the field of chronobiology which deals with biological rhythms and their underlying mechanisms. The second is a branch of psychology. It addresses itself to problems such as time estimation, the emergence of the concept of time in the child, the >time horizon< in normal and abnormal individuals and so on. If one looks upon these as purely cultural matters and if one favors a radical rupture between the biological and the cultural, the question of the relation between the two levels becomes irrelevant. If, on the contrary, one adheres to the evolutionary view, it is important to look for some continuity between successive levels of temporality, and to trace back to their biological roots the origin of behaviors and ideas related to time in humans. Human beings exhibit some pragmatic organization of time or time allocation in their daily life, they show capacities for elaborate cognitive treatment of temporal information, they build conceptual constructs about time, and they experience time with various affective connotations (*temps vécu* or subjective experience of time). Do all these emerge from more basic and more general forms of adjustments to time in living organisms, such as biological rhythms? And if so, how do they emerge? Students in the field of the psychology of time have, with a few exceptions (see Fraisse, 1967; Macar, 1980), neglected the issue. Even Piaget, in spite of his repeated emphasis on the essential continuity from the biological to the psychological and logical levels, did not pay much attention to concepts and data from chronobiology when he dealt with the ontogenesis of the time concept (Piaget, 1968). Some fifteen years ago, the senior author (Richelle, 1968) first advocated a synthetic approach that would bridge the gap between chronobiology and the psychology of time. The mutual ignorance in which these two fields held one another was all the more surprising because the study of time has otherwise been the locus of unusual multidisciplinary cross-fertilization. It was argued that an attempt at such a synthesis would inevitably imply a comparative approach, and would profitably gain from the experimental analysis of temporal regulations in animals.

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The term *temporal regulation*, as we have come to use it for several years, refers to all forms of behavioral adjustments to time, as exemplified by discriminations of duration of external stimuli, entrainment of motor responding in periodic schedules of reinforcement, temporal patterning of distribution of one's own responses, and the like (for a review of the available techniques and of the related problems, see Richelle & Lejeune, 1980). Since Pavlov's initial work on delayed, trace, and periodic conditioning, the study of time estimation and timing behavior in experimental animals has developed tremendously, due to the techniques of the operant laboratory designed by Skinner in the thirties, and constantly improved by his followers. However, important aspects of the problem have been neglected, and in spite of recent encouraging efforts to integrate various subfields in the psychology of time and to link them to chronobiology (see, for instance, Gibbon & Allan, 1984), a general theory of time in behavior and mind remains a far cry.

We do not intend to propose such a theory here. Instead, we shall focus on three questions which seem of special relevance to the general issue of the relations between *biotemporality* and *nootemporality*, and for which empirical answers, be it at an embryonic stage, are becoming available.

(a) *Temporal Regulations of Behavior and Biological Rhythms*. What is the relation, if any, between temporal regulations as studied in behavioral laboratories, which involve adjustments to arbitrary durations usually of the order of a few seconds or minutes, and biological rhythms rooted in ›natural‹, more fundamental periodicities? Do temporal regulations derive from biological rhythms? Do they obey the same underlying mechanisms or do they, on the contrary, correspond to quite different adaptation processes? Do temporal regulations of behavior possibly serve to make the organism free from chronobiological constraints?

(b) *Cross-species Differences and Similarities*. How do various species compare with respect to their timing capacities as assessed with behavioral techniques and ›arbitrary‹ durations (that is, not directly related to biological rhythmicities)? Are structurally simple and highly complex organisms equally endowed with such capacities as they seem to be with circadian or circatidal time keeping mechanisms? And, if this is not the case, is there some (bio)logical order to be found in the differences between species? Is there any ›evolutionary trend‹ detectable, that might lead us to account for the higher levels of nootemporality that characterize human behavior?

(c) *Ontogenesis*. Like any functional capacity of living systems, the question arises as to whether temporal regulations of behavior are merely the actualization of some innate basic competence, or are the result of a shaping of behavior by environmental conditions. A clear answer to this question can only be given by combining behavioral genetics and the ontogenetic approach. The latter also recommends itself if we want to understand the performances observed in mature subjects. Applied to humans, it should not only help us in following the deployment of cognitive capacities with respect to time, but also, by comparing with infrahuman

organisms, in accounting for the crucial differences, if any, that make human time specifically human. Ontogenetic studies in animals are, of course, in that perspective a necessary complement to human studies.

We shall review some of the available facts and comment on selected examples of research in each of these three areas.

Temporal Regulation of Behavior and Biological Rhythms

A few years ago, we reviewed the literature dealing with the relations between temporal regulations and biological rhythms (Richelle & Lejeune, 1980). The number of relevant studies turned out to be extremely small. Only seven or eight references could be located, which reflects the general neglect of chronobiological variables by behavior analysts. Hobbs (1981) also denounced this neglect and pointed out that most experimenters do not care to give details about the maintenance and experimental lighting conditions, nor do they adapt the light-dark cycle to the species-specific habits of their animal subjects. Rats, though nocturnal animals, are usually tested during the day and are kept in the dark by night. Quoting Hobbs: ›not only are we developing a psychology based extensively upon the rat, but one based upon ›sleepy‹ rats as well‹. Curiously enough, even the behavior analysts who had engaged in the study of temporal regulations had, for years, shown no interest in the contribution of chronobiology.

A more recent review by Terman (1983) produced evidence of a somewhat increasing systematic interest in circadian periodicities as related to operant behavior: the list of papers referred to comes close to 20, most of them deriving from Terman's own pioneering research group. Terman is concerned with a more general issue than the one to which we are addressing ourselves here, namely the relation between biological rhythms and behavioral measures in general, not specifically temporal regulations. Circadian rhythmicity has been shown, for example, for responding reinforced by electrical brain stimulation in rats (Terman & Terman, 1970, 1975, 1976), for key-pecking reinforced by light in pigeons (Ghiselli & Thor, 1973), for visual detection thresholds (Rosenwasser et al., 1979). That various behavioral performances obey similar laws as physiological parameters traditionally measured in chronobiological studies should cause no surprise. Such data provide the required baseline against which experimenters can test the effects of manipulating crucial variables in behavioral control (schedule parameters, reinforcement magnitude or frequency, and the like). Especially suggestive in this respect are results obtained on a light-dark 12 : 12 hour cycle, by Zimmerman (Note 8, reported by Terman, 1983). Lever pressing for electrical brain stimulation was recorded throughout, as well as drinking. Inversion of the light-dark cycle resulted in gradual phase adjustment. Then the electrical brain stimulation was set at a higher, more rewarding, intensity during light periods. This produced an immediate shift of operant activity from dark periods to light periods, while drinking remained synchronized with darkness. An environmental condition known to exert important control of behavior, that is, reinforcement magnitude,

can invert the rhythmicity of schedule controlled behavior and make it independent of other activities, such as drinking, that will continue to show the usual pattern. Rats were, so to speak, forced to take their pleasure during day time, quite contrary to the very nature of these nocturnal creatures. This experiment can serve as an experimental paradigm for research on the relation between biological rhythms and behavior, with the following general question in mind: To what extent can environmental contingencies counteract the natural periodicities that affect behavior, as they affect many other aspects of an organism's functioning?

Elsmore & Hursh (1982) have adopted an econometric approach to this question and contributed several ingenious experiments in which total daily food ration, availability of alternative sources of food, frequency of reinforcement, response cost or effort, and proximity to reinforcement were manipulated. They make a distinction between quantitative and qualitative aspects of behavior. *Quantitative* refers here to rate or frequency, *qualitative* to aspects not necessarily related to rate or frequency, such as accuracy in a discrimination task. Both aspects exhibit rhythmicity, but while the former is sensitive to manipulation of variables such as those mentioned above, the latter is not. This contrast was shown, among other situations, in an experiment in which monkeys had to count their own motor responses up to 10 to 15 in order to be reinforced.

Some of the experiments reported by Terman and by Elsmore & Hursh are relevant to the more specific issue that is our concern here. Zimmerman, in the experiment discussed above, delivered the electrical brain stimulation according to a schedule of Differential Reinforcement of Low Rates (DRL) 15 s. In that schedule, a subject is required to space its motor operant responses by at least 15 s if it is to be reinforced. If a response is given too soon, the timer is reset. In the normal conditions (median intensity reinforcement), in which operant activity was much higher during the dark part of the light-dark cycle, the Inter-Response Times (IRT) distribution showed better adjustment to the temporal requirements during dark periods than during light periods. Elsmore & Hursh also trained rats to discriminate the duration of auditory stimuli, long or short, with three levels of difficulty. Animals were tested every 3 hours under a light-dark 12:12 hour cycle. Both accuracy and rate of activity (as assessed by the number of trials completed) exhibited rhythmic fluctuations.

Submitting animal subjects to tests involving temporal regulations at regular intervals around the 24 h cycle, both in light-dark and constant conditions, is obviously a straightforward procedure for gathering data concerning the interaction between the circadian clock(s) and the capacity to adjust to arbitrary durations. An experiment of that type carried out in our laboratory illustrates the experimental strategy and provides some preliminary results (Perikel et al., Note 7). Naive female wistar rats were housed in isolated compartments, consisting of a home cage and an adjacent conditioning chamber. Water was available permanently in the home cage. They were exposed to a light-dark 12:12 cycle (light from 0630 h to 1830 h). After one week of habituation in these quarters, the subjects were food-deprived and shaped to press the lever for food. They were then run for 15 consecutive days on a continuous alternation of 30 min conditioning sessions and 90 min rest periods.

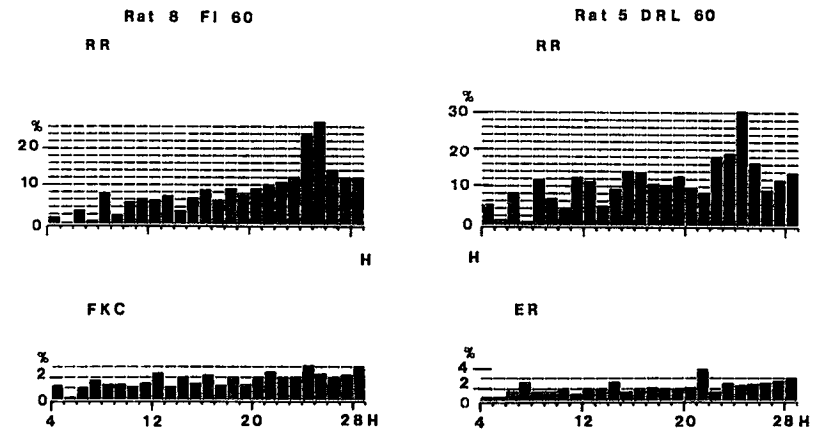


Figure 1. Periodograms of individual Wistar rats in Fixed Interval (FI) 60 s (left) and Differential Reinforcement of Low Rates (DRL) 60 s schedules (right), computed after the root-mean-square-amplitude method (Enright, 1965 a, b). Periods tested range from 4 to 28 hours (abscissa). Ordinates give, in percentage, an estimate of the importance of the rhythmic fluctuation for each parameter considered and at each period tested. The higher the block column at a given period, the more evident is the rhythmic fluctuation of the parameter. *Upper line*: Response rate (RR) for each schedule; *bottom line*: qualitative indices (FKC: Curvature Index of Fry et al., 1960; ER: Efficiency Ratio, i.e. the ratio between reinforced Inter-Response Time and total Inter-Response Times) (from Perikel et al., Note 7).

Some subjects were exposed during the conditioning sessions to a Fixed Interval (FI) 60 s schedule. In this schedule, the time that must elapse before a response can be reinforced remains constant from one interval to the next. The other subjects were exposed to a schedule of DRL of 60 or 30 s. Lever pressing responses were reinforced by food pellets, and conditioning sessions were signalled throughout by an auditory stimulus (white noise). Some individual subjects were submitted to additional manipulations: extension up to 60 days, reduction of amount of reinforcement, removal of auditory signals. Discrimination between conditioning and rest periods was learned within 24 h in FI, within three days or so in DRL. Periodogram analysis revealed a rhythmic fluctuation with periodicity close to 24 h in response rate (much more pronounced in subjects submitted to 60 days of experimental conditions, but already apparent after 15 days), but no such periodicity for qualitative indices of temporal regulations (curvature index in FI; efficiency index in DRL) (Figure 1). This is in line with Elsmore & Hursh's distinction between quantitative and qualitative aspects of performance. One remarkable byproduct of this procedure, in some subjects, has been the development of highly efficient low responding patterns under FI contingencies, their performance resembling a well adjusted DRL behavior, with a ratio of responses to reinforcement less than 2 (Figure 2). This induced >quasi-DRL< performance under FI contrasts with the poor performances obtained from those

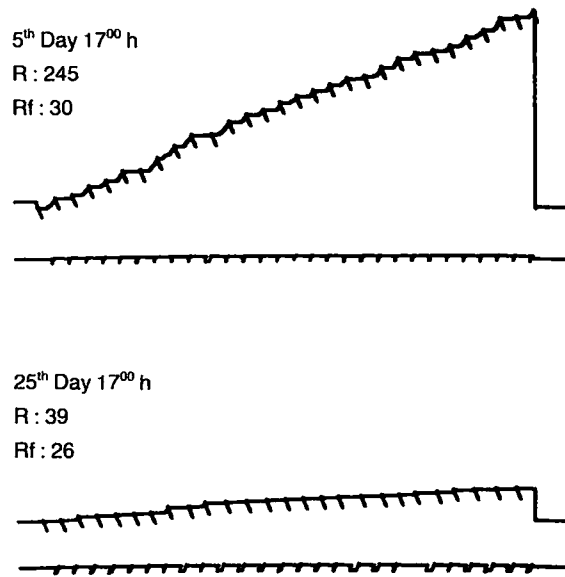


Figure 2. Cumulative records of responses for one individual rat under the Fixed Interval 60 seconds schedule, in experimental sessions starting at 1700 h on days 5 (top) and 25 (bottom), that is the 50th and the 290th session, respectively. Number of responses emitted (*R*) and number of reinforcements obtained (*Rf*) are given in the figure. Downward pips indicate reinforcements on the cumulative graph, and reinforcement disponibility on the horizontal lines under each record. The abscissa corresponds to the duration of the session, that is, 30 minutes (from Perikl et al., Note 7).

rats run under DRL 60 s contingencies. These results illustrate once more, in a particularly clear way, the long-noticed paradox of spontaneous regulation observed under FI contingencies as opposed to the required spacing of responses for comparable delays under DRL.

Another potentially fruitful approach to elucidate the relation between biological rhythms and acquired temporal regulations of behavior, as suggested earlier (Richelle, 1968; Richelle & Lejeune, 1979, 1980), consists in testing the performance under FI contingencies, contrasting time intervals approximating the 24 h period with arbitrary shorter or longer intervals. Such studies give some insight in an animal's capacity to free itself from the basic biological periodicities. Bees visit with remarkable timing accuracy places where food has been available at a given hour each day. However, their sense of time, which is legendary in the chronobiological literature, is exhibited only if the interval between successive food presentations is close to the circadian period. Attempts to train them on FI 60 s have failed to reveal any spontaneous timing, so common among birds and mammals

(Grossman, 1973) (but see the following section for reservations about limited investigations of a given species in comparative studies). Increased freedom from natural periodicities was suggested by Richter (1965; see also Michon, 1985a, chapter 2 of the present volume) as an evolutionary trend leading to an increased flexibility and independence in the various time keeping mechanisms at work in an organism.

Studies on food availability and anticipation of food throw some light on this issue (Boulos & Terman, 1980; Aschoff, 1984; Rosenwasser et al., 1984; Fery, Note 1). When rats are fed *ad libitum* under light-dark 24 h cycles or under constant light conditions, they show eating periods fairly well synchronized with activity phases.

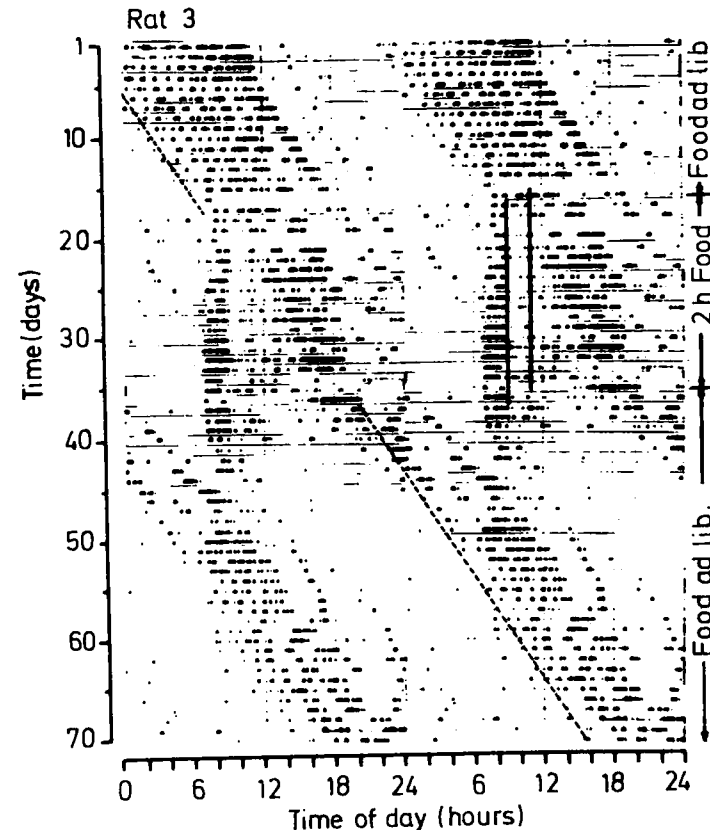


Figure 3. Wheel running activity of an individual rat kept in constant dim illumination (0.2 lux) and alternatively fed *ad libitum* or for two hours per day (between 0900 and 1100 h – see vertical lines to the right in the diagram). Experimental days are indicated on the left ordinate, time of day on the abscissa of the duplicate charts. Feeding conditions can be read on the right ordinate. During the restricted feeding period, a dissociation can be seen between wheel running anticipatory to food and wheel running that freeruns as in the preceding and following *ad libitum* feeding periods. (Adapted from Honma et al., 1983).

Eating is entrained, as is motor activity, by light synchronizers, and exhibits circadian rhythmicity when the synchronizer is removed. If feeding is restricted to limited periods during the 24 h cycle, anticipatory activity will occur prior to feeding time. This anticipatory activity persists under constant conditions, showing a dissociation from circadian activity. Rats can also anticipate meals spaced by intervals close to 24 h, viz. 23 to 27 h, but they seem unable to anticipate if the interval is outside this range. Though the anticipatory mechanism adjusts to the periodicity of environmental events that can be out of phase with circadian endogenous rhythms, it seems to exhibit circadian properties itself since it does not work for intervals differing markedly from the 24 h cycle. Figure 3, reprinted from a study by Honma et al. (1983), illustrates the basic effect of restricted feeding procedure under constant light conditions in rats.

There are other remarkable features about this anticipatory activity. It is observed in situations where the meal is offered irrespective of the animal's behavior as well as in situations in which food is contingent upon responses. In other words, restrictive feeding may be scheduled according to a Fixed Interval program or to a Fixed Time program (Pavlovian periodic conditioning). It also shows the acceleration pattern that is typical of response rate in FI schedules. At first sight a simple process of temporal conditioning might plausibly account for the anticipatory activity and make it quite distinct from circadian rhythms. The fact that it survives suprachiasmatic lesions is another argument to the same point (Phillips & Milkulka, 1979; Suda & Saito, 1979; Boulos et al., 1980; Stephan et al., 1979a, 1979b; Stephan, 1981, 1984). In mammals, the suprachiasmatic nuclei are, at present, the most serious candidates for neural control of circadian rhythmicity (see Rusak & Zucker, 1979; Groos & Daan, 1985, chapter 4 of the present volume). Innis & Vanderwolf (1981) have investigated the effects of suprachiasmatic lesions on circadian rhythms of running activity and on short FI performance in rats. While they were able to obtain the now classical disruption of circadian rhythms, FI patterns remained unaltered, as did anticipatory activity. However, other features paradoxically contrast anticipatory activity with temporal regulations as observed under FI schedules. Available evidence shows that anticipatory activity occurs only for intervals approximating 24 h between restricted feeding periods. It persists for several days after *ad libitum* conditions have been reinstated. According to Terrian et al. (1984), anticipatory activity involves a circadian oscillating mechanism rather than a *scalar timer* which is supposed to control temporal regulations; a scalar timer can be reset at any point (e.g. Gibbon, 1977).

The relations between the timing system involved in anticipatory activity and the system underlying FI type behavior are only beginning to be explored (Terrian et al., 1984; Fery, Note 1). Figure 4 gives an example of the type of procedure that can be used. The strategy essentially consists of making food available on a restricted feeding program and contingent upon the subject's activity. This amounts to programming the meals according to a FI schedule, the interval being chosen within the 22 to 27 h range that is known to be critical for anticipatory activity to occur. The interval is then progressively shifted to shorter values, to see if the circadian constraints on anticipatory activity can be removed.

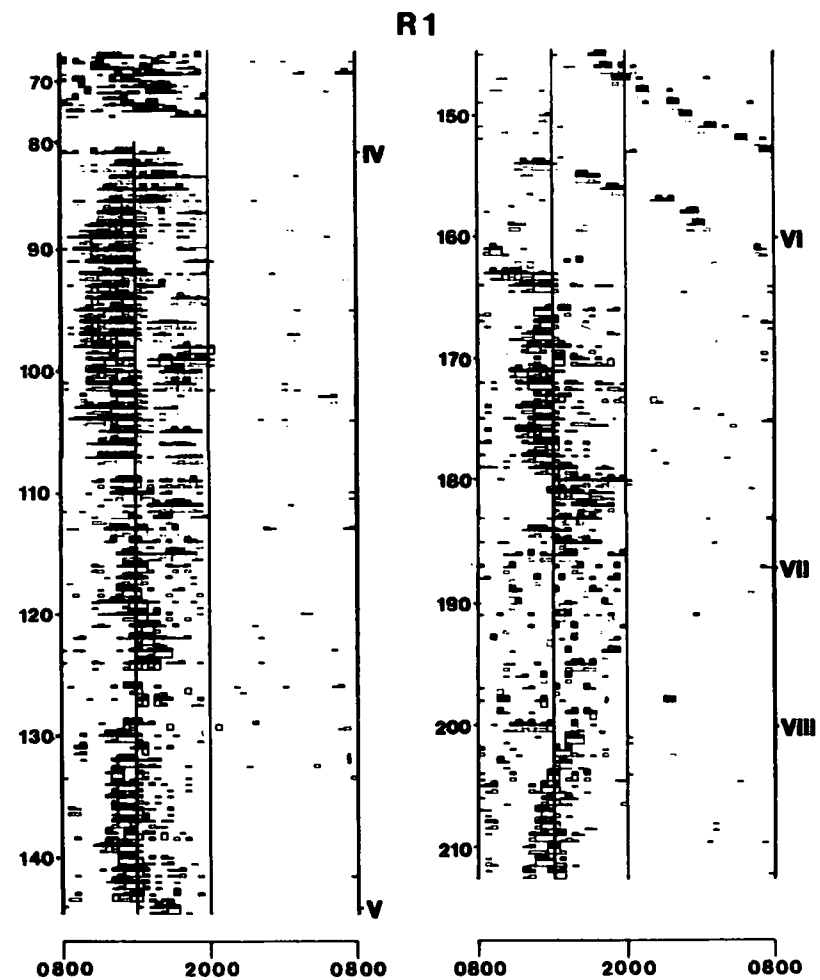


Figure 4. Quartile plots of lever pressing activity (filled symbols) and wheel running activity (empty symbols) under a conjunctive FI 24 h FR 50 schedule in one individual rat (R1) over successive experimental phases, from the top left to the bottom right. Prior to phase IV, the rat was exposed to a light-dark 12 : 12 h cycle under an *ad libitum* feeding schedule with no access to the lever; only the wheel running activity was recorded. In phase IV, the reinforcement was available every 2 h and for a 18 h availability period; it was delivered only after 50 responses had been emitted. In phase V the subject was maintained in constant dim light and under the same reinforcement schedule. Phase VI was like phase IV. In phase VII *ad libitum* free access of food was provided. Phase VIII was like IV and VI. The height of each symbol is proportional to the activity displayed per 30 min period. Successive experimental days are indicated at the left side of each chart. The thin vertical line halfway between the 0800-2000 h period indicates the occurrence of reinforcement disponibility in phases IV, V, VI and VIII where the reinforcement schedule was in effect, or the moment at which it should have occurred during the *ad libitum* feeding phase (VII). Note the anticipatory pattern, in running wheel activity as well as in operant lever pressing activity, induced by the schedule of reinforcement in phases IV, V and VIII, and simultaneous free running of both activities in phase V (after Fery, Note 1).

This line of investigation is certainly promising for our understanding of the relative independence and the possible interactions between biotemporality and individually learned temporality. It is clear, however, that the evolutionary significance of this kind of analysis can appear only if it is framed in a consistent cross-species approach, relating temporal regulations to learning mechanisms and their neural substrate. It is to this approach that we shall now turn.

Cross-species Comparisons

On earlier occasions (Richelle & Lejeune, 1979, 1980, 1984) we have proposed and discussed three hypotheses concerning the distribution of the capacity for temporal regulations among various animal species: the *egalitarian-reductionist* hypothesis, the *ethological* and the *evolutionary* hypothesis.

According to the egalitarian view, all species would be equally endowed with capacities for temporal regulations, as they are for circadian or/and other biological rhythmicities. Observed differences would result from inadequate selection of experimental variables, making the situation non-equivalent for different species. The ethological hypothesis accounts for interspecific differences by pointing to the typical ecological conditions under which each species has evolved; it emphasizes the notion of species-specific constraints on learning. The evolutionary hypothesis assumes that the capacity for temporal regulations obeys some general trend, possibly parallel to the increased complexity of nervous structures, or to the increased potentialities for learning. The labels used are admittedly crude and somewhat oversimplifying, but they nevertheless correspond to three lines of interpretation that are current in psychobiology and behavioral research. There are, of course, important problems as to the relations between them. For instance, the ethological view might be looked at as more akin to a true evolutionary explanation than the view defined here as *evolutionary*, which could be more appropriately labelled *anagenetic*. For our present purpose we may forget these problems.

It would seem that the egalitarian hypothesis could be ruled out if the dissociation of (at least) two different classes of timing mechanisms, as suggested in the preceding section, could be confirmed. However, until such confirmation is obtained, it is heuristically advisable to question any interspecific difference by suspecting ›unfair‹ experimental conditions with respect to the species-specific behavioral repertoire. The concern for designing ›species-fair‹ tests is shared, though for quite opposite reasons, by advocates of the ethological view. Since temporal regulations as we define them are aspects of learned behavior, they can be looked at in the general framework of learning mechanisms and evolution. Current theorizing goes to the extreme view that there is no general universal learning mechanism, but that there are, in the limit, as many learning processes as there are species that learn different things under different conditions (Plotkin & Odling-Smee, 1979, 1982).

As a research strategy, the evolutionary view recommends itself by being clearly open to refutation. It expects, in temporal regulations as in other things, interspecific differences that can be described as an ordered trend in the same way

as, in a given phylum, species can be ordered without any teleological implications, according to the number of neurons or to the encephalization quotient. Experiments can then be designed, based on the egalitarian or on the ethological hypothesis, for demonstrating either that the alleged differences are not real (viz. they fade out when another procedure is used or when another behavior is looked at), or that they show no trend but merely reflect the irreducible species-specific styles of adaptation. Adopting that research strategy does not, of course, relieve the experimenter from the task of asking an animal the sort of question it can understand, that is, selecting appropriate responses, reinforcers, stimuli, housing conditions, and so forth. It is also important to note that an evolutionary trend in temporal regulations may not show up in simple measures of behavior, such as the waiting time in a FI or DRL schedule, or the accuracy of time discrimination. It

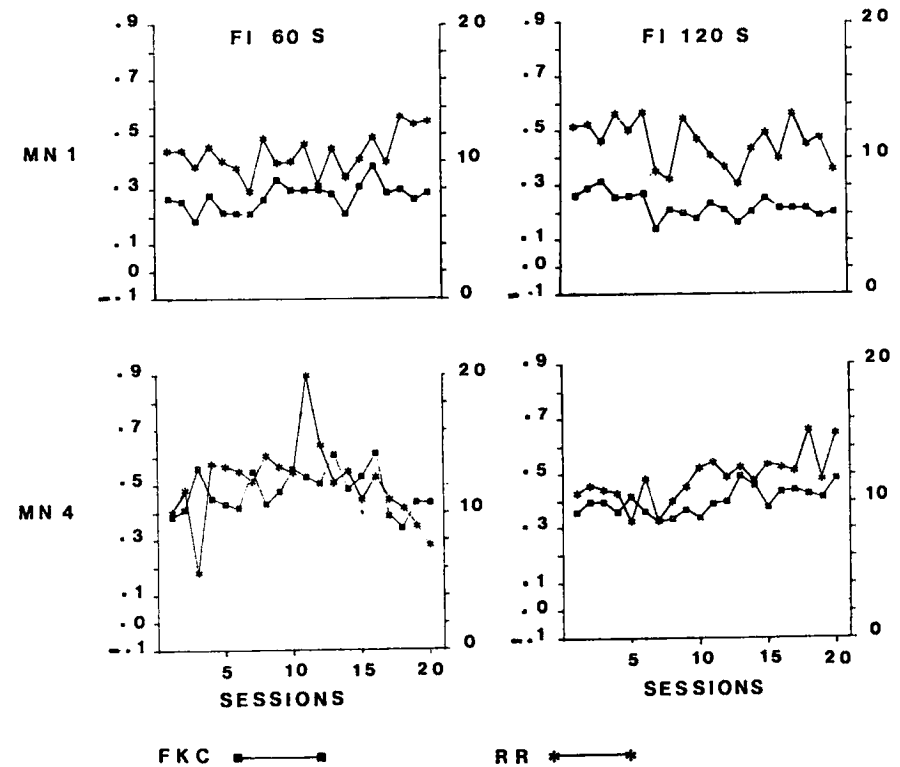


Figure 5. Evolution of performance of two individual fish (MN1 and MN4) of the species *Sarotherodon niloticus* under Fixed-Interval contingencies (FI 60 s and FI 120 s). Curvature index (FKC) and running rate (RR) — on the left ordinate scale and right ordinate scale respectively — are plotted as a function of session (abscissa). The curvature index has been computed on distributions of responses in ten successive segments of the interval; it can take values from -0.9 to $+0.9$ (usually only positive values are obtained). The running rate is the average rate of responses per minute in the ›active‹ phase following post reinforcement pause (from Grailet, Note 2).

might be observable only when more complex dimensions of behavior are considered, such as flexibility in adjusting to various, rapidly changing temporal requirements or capacity to exhibit concurrent temporal regulations, and the like.

Whatever one's theoretical inclination, data are needed on a reasonably large sample of species if the issue is to be tested. The data available at present are far from sufficient for any coherent picture to emerge. From what we know, there is some hint that mammals rank highest (monkeys, cats, rats, and mice being the main species studied), followed by birds (mainly pigeons), fishes and reptiles in that order (see Richelle & Lejeune, 1984). Taking the phyletic scale in a simplistic way, one would expect to find reptiles ranking higher than fishes. But the number of species studied in these two groups, as well as the number of studies on any given species, is insufficient.

Figures 5 and 6 show samples of typical individual performances in one species of fish (*Sarotherodon niloticus*) and one species of reptile, the fresh water turtle (*Pseudemys scripta elegans*). The tropical fish shows evidence of temporal

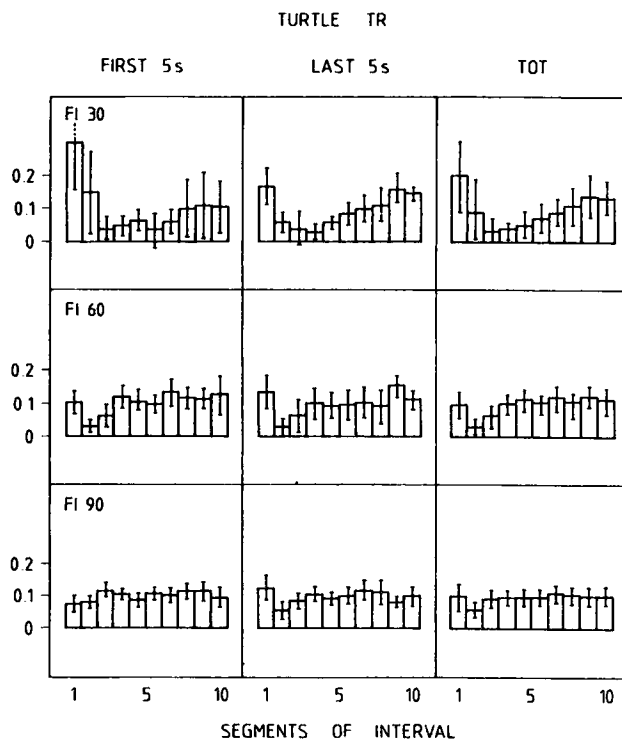


Figure 6. Relative frequencies distributions of responses in successive segments of the interval for FI values of 30, 60 and 90 s in an individual subject of the species *Pseudemys scripta elegans*. Average values are shown for the first five sessions (*left*) the last five sessions (*center*) and all sessions (*right*, 15 or 20 sessions) (from Laurent, Note 3).

regulation typical for the FI schedule (60 and 120 s), though qualitatively poorer than tends to be observed for the usual laboratory animals. The best subjects had a score between 0.3 and 0.5 on the so called curvature index (Figure 5). While the fish performed moderately well, the water turtles did not exhibit any evidence of temporal patterning of their responses even after having been exposed to the FI schedule (30, 60 and 90 s) for more than 100 sessions. Their curvature index remained between 0.003 and 0.18 (Figure 6).

One may wonder whether the experimental conditions were appropriate to the characteristics of these species. Provisions were made, of course, to adapt the situation to the animals. The fish were kept in individual watertanks, where they were trained to push with their head on an immersed lever. The turtles were housed in an aquaterrarium, and isolated for the period of a session in the conditioning chamber in which they were trained to push a specially designed lever with their head or paw for food reinforcers. At first sight, there is no reason to suspect the selected response to be more artificial or inappropriate than the familiar lever pressing of laboratory rats: subjects did learn it easily. The fish have also been trained without any difficulty to put the response to use under other schedules of reinforcement not involving temporal regulation. Other important variables, however, may have been responsible for their poor performance in this case. The feeding schedule involved in FI contingencies may not be compatible with feeding habits of *Pseudemys scripta* and thus account for its unexpectedly poor temporal patterning. It remains to be demonstrated, therefore, that digestive physiology has not obscured timing competence in this particular case.

That a change of response or of some other variable suffices to produce drastically different performances in conditioned behavior has been widely documented in the 10 years since the investigators' attention was first drawn to the so called biological constraints on learning.

Key pecking in pigeons has been subjected to close scrutiny, with the result that the notion of arbitrariness of that particular operant (and possibly of any response selected by the experimenter) had to be abandoned definitively. Pecking, because of its status in the natural repertoire of preparatory and consummatory eating behavior, was initially expected to be amenable to control by contingencies that require temporal regulations. The observed limitation on the pigeon's capacity to space pecking by more than 10 to 15 s in a DRL schedule has become a classical illustration of a species-specific constraint, and explains why experimenters began to look for some other responses that would more reliably reveal true timing competence of pigeons. Somewhat better performances have indeed been obtained with treadle pressing (Hemmes, 1975; Mantanus et al., 1977) but this is a rather unnatural motor response for birds. We have explored another operant, namely sitting on a perch. Can pigeons, obviously unable to space their pecks by a given delay, keep perching for that duration? In a study reported earlier (Lejeune & Richelle, 1982) pigeons were trained to perch for durations up to 50 s in order to get food. The reinforcer was presented only if the bird jumped off the perch after the critical duration had elapsed. This schedule of Differential Reinforcement of Response Duration (DRRD) produced excellent timing as evidenced by IRT

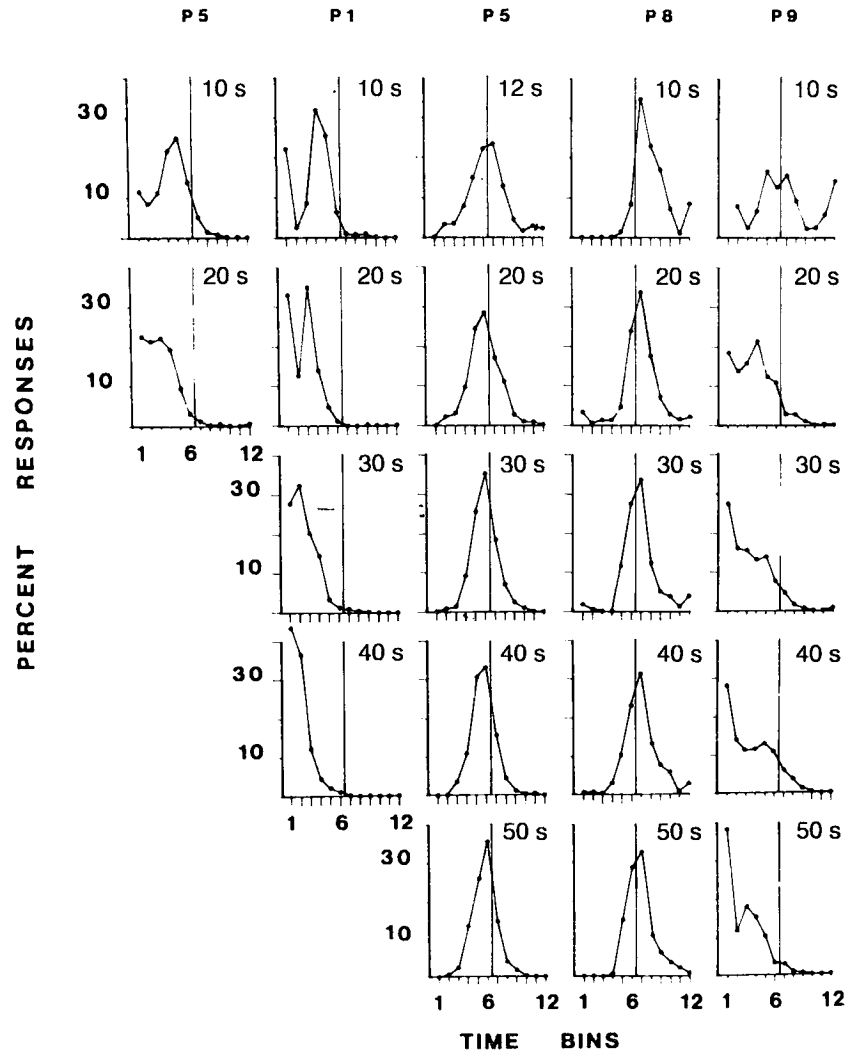


Figure 7. Temporal regulation of operant motor behavior as a function of the response topography and the schedule characteristics in pigeons. From left to right: bird P5 under differential reinforcement of low rates (DRL) of key pecking; bird P1 under DRL of treadle pressing; bird P5 under differential reinforcement of response duration (DRRD) for perching; bird P8 under DRL of brief perching responses; bird P9 under the same conditions – to which it was shaped and maintained for the 10s delay – switched to >neck stretching< response from 20 s on. Critical value of the temporal parameter is indicated on each graph in which relative frequency is plotted as a function of the interresponse time or response duration class. Each step on the abscissa corresponds to one sixth of the critical values, marked by the vertical line. Interresponse time (or response durations for central column) were recorded over the 3 last sessions out of 20 at each schedule values for birds P1, P8 and P9, over 3 sessions at 10 and 20 s and over the 3 last sessions out of 15 at 30, 40 and 50 s for bird P5 (see Lejeune & Richelle, 1982).

distributions, illustrated by bird P 5 in the third column of Figure 7. This contrasts sharply with key pecking performances, in which spacing of responses hardly matches the critical value beyond 10 s, as illustrated for the same individual in the first column of Figure 7. The same procedure was applied to turtle doves, with the same outcome (Richelle & Lejeune, 1984). Pecking under DRL is not, therefore, a valid procedure to uncover the timing capacities of these two species. One might object, however, that the schedule factor (DRRD versus DRL) was more important than the type of response as a determinant of the difference, as was pointed out by Fantino (1984).

A recent experiment (Lejeune et al., Note 4) provides a solution. It compared DRL performance in pigeons using two topographically distinct operants, treadle pressing and discrete, brief perching. Reinforcement, in both cases, was contingent upon minimal spacing of responses. The critical delay was progressively increased from 35 to 40 s (for treadle pressing) or 50 s (for brief perching) in 15 steps. Eight adult homing pigeons served as subjects in this experiment. Interresponse time distributions for one bird in each group (P1 and P8 respectively) are presented in Figure 7. Other subjects showed similar results with one exception that will be discussed below. Treadle pressing performance, supposedly slightly better than keypecking, is far from matching the DRL requirement. Brief perching, in sharp contrast, produces symmetric distributions, with a mode coinciding with or slightly longer than the critical delay. Bursts of responses with short interresponse times are clearly eliminated by the particular topography of perching, but such bursts alone cannot explain the poor timing obtained with treadle pressing or pecking. Figure 8 shows the median interresponse times or response durations plotted against the critical values for typical individuals in each condition. Up to 50 s, perching birds exhibit excellent performances, compared with treadle pressing. Efficiency ratios remained high (above 0.40) for perching subjects and for all delay values, while they fell from between 0.20 and 0.30 to less than 0.10 for the other birds.

An interesting case is offered by bird P9 in the perching group, whose results are also shown in Figure 7 and 8. Its performance is similar to that of the treadle pressing birds. In fact, after initial shaping of the common perching response, this bird shifted to a different strategy consisting in pushing the perch down with its neck, thereby achieving the same mechanical effect as it would by jumping on it. This shift took place between training on DRL 10 and 20 s, so that results shown are for >neck stretching<, except at 10 s. The various parameters of its performance shifted accordingly.

These results clearly demonstrate that response topography, not the schedule, is the crucial factor in the differences observed between perching and key pecking, or treadle pressing. That brief perching responses of birds can be spaced in time just as well as lever presses in rats is an intriguing observation, especially if we compare it with the relatively poor treadle pressing performance, a response that seems no less >natural< for birds than key pecking. Intriguing is also the idiosyncratic behavior developed by bird P9. Possibly, neck stretching and pushing are topographically quite close to key pecking and equally resistant to temporal control. Watching the birds in the conditioning chamber revealed the peculiar preparatory activity

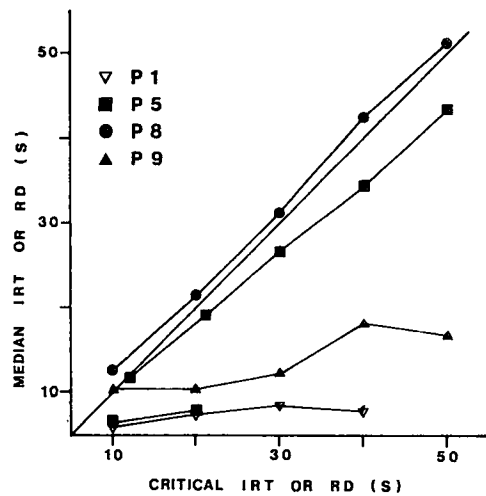


Figure 8. Median Inter Response Times (IRT) or response durations (RD) as a function of the critical IRT or RD value and response topography in pigeons. From top to bottom, birds P8 under DRL of brief perching (●), P5 under differential reinforcement of perching duration (■ from 10 to 50 s), P9 (▲) under DRL of brief perching (at 10 s) followed by DRL of >neck stretching< (from 20 to 50 s), P5 under DRL keypecking (■ at 10 and 20 s) and P1 under DRL of treadle pressing (▽ from 10 to 40 s). Data are computed as in Figure 7. Points would have fit with the diagonal line in the case of perfect matching between median values and schedule requirements.

exhibited by the perching birds: movements of the paws and of the neck (stretching upward) preceded jumping onto the perch. This anticipatory activity seemed to build up until the >decision to jump< was made. These movements were not observed prior to jumping in the home cage, where a similar perch was also available.

This example of within species comparison in temporal regulations as exhibited with different motor behaviors illustrates the complexity of the cross-species approach. What performance or performances should we retain as revealing the underlying timing competence in a given species? Should we systematically explore the essentially unlimited range of responses, reinforcers, stimuli, etc., and characterize the animal's capacity on the basis of its best performance? Or should we, perhaps more appropriately, evaluate an animal's ability to apply its clock(s) to a variety of responses and situations with equal efficiency? Does it make sense to dissociate a hypothetical underlying clock and the temporally regulated behavior, to make a distinction between *competence* and *performance*? Why not admit that there are as many clocks as there are behaviors exhibiting timing properties and that every behavior is inherently timed? We suggest that those and similar questions remain open to further inquiry. They should not be dodged in the current attempts, perhaps premature, to build conceptual unifying mechanisms.

Ontogenetic Studies

The study of ontogenetic development has proved a fruitful way to gain insight on the organization and the function of behavior. In spite of its long standing and widely recognized merits the ontogenetic approach has been surprisingly neglected in the field of time. A few data are available on the ontogeny of circadian rhythms (Davis, 1981). Though circadian rhythms are admittedly controlled by some basic

mechanism of genetic origin, their emergence requires some time in early development. Thus it takes 3 to 4 months in the human infant before the sleep-wake rhythmicity gets organized. In rats, adrenal rhythmicity develops after 3 to 4 weeks; pineal rhythmicity, however, appears much earlier, within 3 to 4 days. Animals need not experience 24 h cycles in their early stages to exhibit circadian rhythmicity as adults. Young mice kept under 20 h or 28 h light-dark cycles show persistence of the induced rhythm when transferred to constant conditions, but only for 15 days or so, after which the circadian rhythm takes over (Davis & Menacker, cited in Davis, 1981).

Not much is known about the development of biological rhythms with aging. In humans, the main trend in old age seems to be a decrease in amplitude that eventually results in the fading out of rhythms. There may also be a change in phase relationships within the circadian system, and a decreased capacity to adjust to time schedule modifications. Maintaining good temporal organization, in the chronobiological sense, would be a warrant for healthy aging. Humans might profitably ponder over some experimental data obtained in insects. The life of flies is shortened when they are exposed to unusual periodicities, that is, to schedules differing from the 24 h cycle, or constant light, or to phase shifts simulating jet lags (Aschoff et al., 1971; Saint-Paul & Aschoff, 1978).

At another level of the study of time, the ontogeny of time estimation and of the time concept has been extensively studied since Piaget's pioneering contribution (Piaget, 1946). Most of this research, however, starts after the *infant* stage, when the human subject begins to master symbolic and linguistic tools. There are good reasons to assume that language is causing changes no less significant here than in the other areas of behavior and cognition. What, precisely, makes the difference cannot be assessed unless we know something of the infant stage on the one hand, and of development in non-speaking animals on the other. Temporal regulations of behavior in the human baby are being currently explored by Pouthas, whose approach and data are illustrated in chapter 6 of the present volume (Pouthas, 1985). We shall concentrate here on studies of animal development.

To our knowledge, no study has been devoted specifically and explicitly to the exploration of temporal regulations of behavior in animals as a function of age, except for Goodrick (1969) who compared performances of young (that is, 9 to 10 months old) and senescent (28 months) male rats under a FI schedule but who, unfortunately, provided no other measure than overall response rate. Incidental relevant data can be found in a few studies not directly addressing the present question. It was found that newly hatched chickens and ducklings exhibit the typical pattern of behavior generated by FI contingencies (Marley & Morse, 1966; De Paulo & Hoffman, 1981). In squirrel monkeys this pattern is more marked in young (2 to 3 years) than in old (15 years and more) subjects (Harrison & Isaac, 1984).

Systematic developmental studies on temporal regulations have been in progress in our laboratory for a couple of years. In one of these studies (Lejeune et al., Note 5), young quails (*Coturnix coturnix japonica*) are used as subjects. This species is rarely used in operant laboratories (see, however, Reese & Reese, 1962; Cloar & Melvin, 1968), but it recommends itself for our purpose; it is easily

produced in incubators, it is a nidifuge species, it has been extensively described by ethologists and is frequently used in psychophysiological (and more specifically neuroendocrinological) research with important chronobiological implications (Balthazart, 1983; Balthazart et al., 1979). A preliminary study on adult subjects, using key pecking as a response, was run to test general conditionability and behavior under FI schedules up to 2 minutes. Then, a comparative study was undertaken in young and adult subjects. Ontogenetic studies raise technical and methodological problems quite similar to those raised by cross-species studies. Just as one must look for species-fair tests, one must design age-fair situations for young animals. The reinforcer must be adequate (flour was used rather than grain); so must the response (treadle pressing was preferred to key pecking in this exploratory study, because of the difficulty to calibrate the key to the excessively frail beak of freshly hatched quails). The amount of reinforcer as the response determining force must be adjusted as a function of growth.

Any experimenter working on development of acquired behavior is confronted with another universal problem: learning takes time and young organisms grow older every day. Reaching asymptotic stabilized performances in temporal regulations in adult subjects usually requires 30 to 50 daily sessions, including shaping, training to the particular contingencies, bringing to the final value of the critical temporal parameter, and exposing the subject to it long enough to extract valid data. However, quails are mature at about 40 days. Therefore, subjects were run in the conditioning chamber for 30 minutes four or five times per day in this case, so that a reasonable number of sessions could be obtained within twelve days.

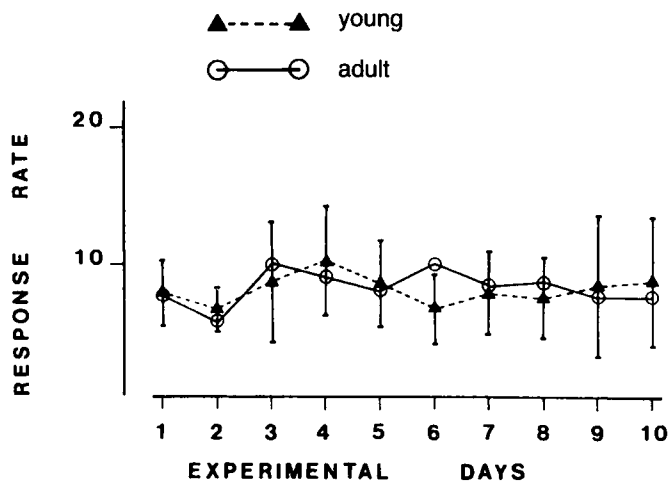


Figure 9. Evolution of response rates over 10 experimental days in two groups of quails of the species *Coturnix coturnix japonica* (young and adult) under a FI 60 s schedule of treadle pressing. Each point presents the daily average of response rates computed for each group over all subjects and over all daily sessions. Standard deviations are given only for the young subjects (7 days old at experimental day 1).

This procedure reduces, of course, the number of subjects that can be run in one experimental unit, so that the results presented here are as yet from a very small number of subjects ($N=10$ for the young group; $N=3$ for adults).

All young subjects were successfully conditioned by the fourth day of life and exposed to FI contingencies from the fifth day on, with the interval increased to 60 s within 8 sessions. Although the response rate of young subjects did not differ from that of adults (Figure 9) the quality of their temporal regulation, assessed by the curvature index was clearly lower, as shown in Figure 10. The young quails improved from day to day and showed evidence of emerging temporal regulation. However, their performance did not match the performance of adults. This could mean that young animals have not yet completely developed their capacity for temporal regulations. More data and controls for a number of variables are needed, however, before such a conclusion can be drawn. Control for the effects of food deprivation on the physical growth of the organism is essential in all ontogenetic studies. By running the subjects several times a day, we may have cancelled these effects to some extent. However, the young animals submitted to conditioning ended with a 15 to 25 percent loss of weight compared to control subjects maintained on an *ad libitum* feeding schedule. A precise description of spontaneous eating habits should provide criteria for choosing intersession intervals and number of sessions per day.

The momentary isolation required by the conditioning sessions may be a source of emotional disturbance interfering with temporal regulations. Although subjects were kept in a group in a compartment adjacent to the conditioning chamber and remained in auditory contact with their fellows when isolated during experimental sessions, this may not have completely eliminated emotional reactions.

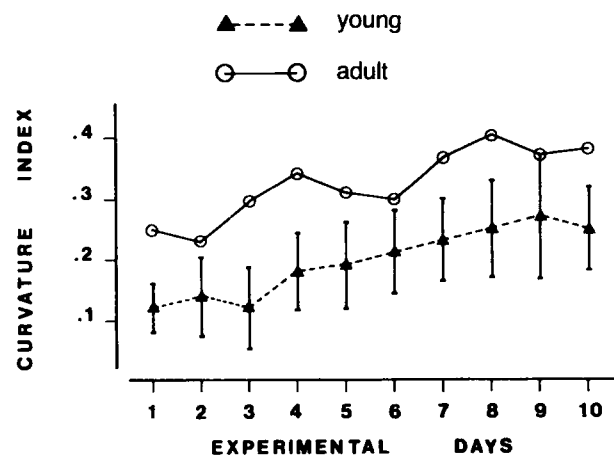


Figure 10. Evolution of the curvature index value over 10 experimental days in two groups of quails (young and adults) under a FI 60 s schedule of treadle pressing. Each point presents the curvature index value computed for each group over all subjects and all daily sessions. See the legend of Figure 9 for other details.

In another study (Lejeune et al., Note 6) young rats tested at time of normal weaning (20 days) were compared for performance under FI 60 s, with senile (approximately 26 months old) rats. The young animals were shaped to press a lever for food by day 21 and then put on FI schedule for five 30 minute sessions per day for 8 consecutive days. Old subjects were naive animals that had been housed individually for about two years. The main results are summarized in Figure 11, which shows that response rate was lower and much less variable, both intraindividually and interindividually, in senile rats than in young rats. In contrast, temporal regulation (as assessed by the curvature index) was less variable in younger subjects. It was clearly better early in training and remained somewhat better throughout the experiment. Young subjects reached values which seniles did not ever attain. Given their initial poor performances, old animals showed considerable improvement but they showed a marked interindividual variability, sharply in contrast with the reduced interindividual variability of their response rate.

The young rats in this study performed much better than young quails but, of course, one must ask the question: How young is *young*? Data for rats were from day 23; those for quails from day 5. What does this difference mean develop-

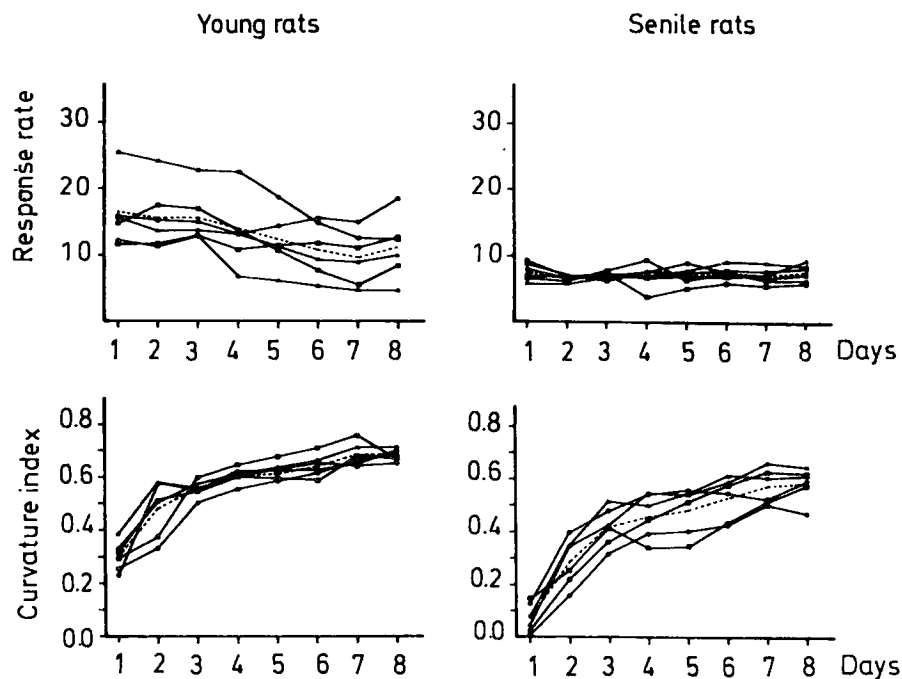


Figure 11. Evolution of individual and group average (broken lines) response rates (upper half) and curvature index values (lower half) over 8 experimental days (abscissa) in 6 young and 6 senile male Wistar rats under a FI 60 s schedule. Each point takes into account the complete daily performance (5 sessions), be it for individual subjects or group average.

mentally? It might be appropriate to derive embryogenic and epigenetic criteria of a morphological nature and to relate behavioral measures to some index of neural development.

However, in the absence of a more sizeable body of empirical data, it seems better to consider some prospects for future developmental research. Restricting ourselves to the behavioral level, we must be aware that the kind of temporal regulation explored in the reported studies is only one among many to reveal developmental properties. If, as we have suggested (Richelle & Lejeune, 1980), temporal regulations involve inhibition depending to various degrees upon the characteristics of the situation, more demanding contingencies should be explored concurrently with FI schedules. If the FI schedule has been preferred as a starting point, it is because it is more feasible and also because it has some relevance to the problem of the relation between periodic conditioning and circadian rhythmicity.

How prenatal and early exposure to a selection of ›arbitrary‹ periodicities (of food presentation, for instance) influence further adjustment to similar periodicities in conditioning situations, is another as yet unexplored line of research that should merge with similar studies on the circadian system of food anticipation. Can ›temporal sets‹ be induced by early exposure? Is there a sensitive period for that induction? To what extent can it go against the ›natural‹ rhythm? Are there, in this respect, notable cross-species differences? We cannot predict the outcome of investigations addressing such questions, but we can foresee their potential relevance to applied problems in humans.

As suggested with respect to species differences, age and development may not be critical with respect to accuracy of temporal regulations, but to the flexibility of timing systems. Research should therefore focus on the capacity of an organism to adjust to rapidly varying delays or to master various delays concurrently. Neither do we know as yet anything about the tolerance as a function of age to temporal contingencies that remain unchanged for a long period of time; but there are a few hints on the possibly aversive properties of constant temporal schedules that should be further explored in young and old subjects. Can young organisms be maintained as long on an arbitrary temporal regulation task as adults or seniles? Speculating a bit more, one might also ask about the advantages or the disadvantages of periodic schedules or regular allocation as a function of age. Is the regular time pattern of classroom activities a source of efficiency and motivation for the child or the adolescent, or does it generate, by its inherent predictability, boredom and loss of interest? Ontogenetic animal studies of temporal regulations may perhaps help us some day in analyzing school situations.

Final Comments

Much of what has been said in the preceding pages is about *Time* in the *Behavior* of animals. What about their *Mind*? In a way, the sort of experiments we have been discussing or suggesting as a necessary path toward a synthetic view integrating

chronobiological, comparative, and ontogenetic aspects of temporal regulations might look alien to the dominant trend in psychological research on time today. Intensive attempts are currently made to characterize the properties of the internal clocks that time behavior in animals and in humans. There is no question about the fruitfulness of such theorizing of which the present volume offers many and convincing examples. Models proposed to account for animal timing capacities are usually based on conceptual and mathematical tools developed in the field of psychophysics of time in humans (see chapters 2, 7 and 13 of the present volume). In that respect, they contribute to the integration of domains unduly kept apart and, in the long run, to a comprehensive theory of psychological time (see Church & Deluty, 1977; Gibbon, 1977; Gibbon & Church, 1981; Gibbon et al., 1984). Such models, however, derive their validity from their applicability to a wide array of empirical facts. But, as we have seen, whole areas of fundamental importance are still *terrae incognitae*. Elaborating highly sophisticated models runs the risk of being pointless if there are not enough data to apply such models to. Thus it is impossible at the present stage to claim wide validity for a model based on the assumption that temporal regulations for short interval are strictly distinct from biological periodicities such as circadian rhythms. We do need a more systematic inquiry on the relations between the two sets of phenomena. Similarly, we cannot contend that »the accuracy of (time) discrimination does not vary substantially among vertebrates« (Roberts, 1983, p. 347) when available comparative data cover no more than a dozen species and hardly support that kind of generalization anyway.

In conclusion, what we want to say is the following. A balance should be maintained between the construction of models for inferred mechanisms and the collection of facts guided by a sense of diversity in nature. Students of time in animals should not abandon simple, straightforward curiosity to guide them. We must explore many more species, many more procedures, many more responses, reinforcers, stimuli, ages, etc. And finally, sticking to the observable may well be for some time to come, an efficient way to reach correct inferences about the clocks inside the animals that might indeed be part of their minds.

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