*Published in Journal of the Experimental Analysis of Behavior (2006), vol. 85, n°1,*
*pp. 125-142*
*DOI: 10.1901/jeab.2006.85.04*
*Status : Postprint (Author's version)*

# About Skinner and time: behavior-analytic contributions to research on animal timing

Helga Lejeune[a], Marc Richelle[a], J. H. Wearden[b]

[a]*University of Liège*

[b]*University of Manchester*

**KEYWORDS**: B.F. Skinner, temporal control, fixed-interval schedules, temporal differentiation, models of timing

## ABSTRACT

The article discusses two important influences of B. F. Skinner, and later workers in the behavior-analytic tradition, on the study of animal timing. The first influence is methodological, and is traced from the invention of schedules imposing temporal constraints or periodicities on animals in *The Behavior of Organisms,* through the rate differentiation procedures of *Schedules of Reinforcement,* to modern temporal psychophysics in animals. The second influence has been the development of accounts of animal timing that have tried to avoid reference to internal processes of a cognitive sort, in particular internal clock mechanisms. Skinner's early discussion of temporal control is first reviewed, and then three recent theories—Killeen & Fetterman's (1988) Behavioral Theory of Timing; Machado's (1997) Learning to Time; and Dragoi, Staddon, Palmer, & Buhusi's (2003) Adaptive Timer Model—are discussed and evaluated.

The present article discusses the contribution of the work of B. F. Skinner, and his legacy of behavior-analytic methods and approaches, to the study of animal timing. What are the main contributions of Skinner, and those who followed the trail he blazed? In our view there are two, and discussion of these two provides the overarching structure of the present work. The first contribution is the development of the operant method, and its use, both by Skinner and colleagues and those who came later, to study a range of issues in animal timing. Pavlovian work that preceded Skinner's (e.g., Pavlov, 1927) had produced good evidence of what would now be called ''temporal control'' in animal behavior, in particular the phenomenon of ''inhibition of delay'' (discussed by Skinner, 1938), obtained when a temporal gap is introduced between the successive presentations of the unconditioned stimulus (US) alone (conditioning to time) or between the onset of the conditioned stimulus (cS) and the US (delay and trace conditioning). In the present article, we will focus on the development of operant methods both in Skinner's own work and that of others, with particular emphasis on what seem to us methodologically important or interesting studies.

The second major contribution of Skinner and the behavior analysts who followed him is theoretical and concerns attempts to account for temporally regulated behavior in animals within a theoretical framework that avoids explanation in terms of events inside the organism, such as internal clocks that can be read directly by the behaving animal. The status of ''time'' as a dimension controlling behavior or an attribute of events that could be perceived directly always has been theoretically troublesome, even within the domain of time perception in humans. Gibson (1975) famously remarked that ''events are perceivable but time is not,'' and Machado (1997) prefaced his own work with a quotation from Piaget to the effect that ''time is not a cause, but a vehicle of causes.'' These aphorisms are elegant and thought provoking, but are less than helpful to people concerned with developing rigorous accounts of how it happens that animals and humans can show sensitivity to temporal properties of events, although both quotations hint at an explanation of timed behavior that involves something other than the direct perception of time itself.

The ''time problem'' can be illustrated with reference to the behavior that occurs under fixed-interval (FI) schedules, one of Skinner's own inventions. On a typical FI schedule, the first response occurring *t* s from the previous reinforcer delivery is itself reinforced, so opportunities to obtain reinforcers are spaced with near-exact temporal periodicity. As is well known (Ferster & Skinner, 1957), exposure to FI contingencies results, after a few tens of sessions of training, in temporally differentiated behavior, with little or no responding occurring early in the interval, and increasing response rates (observable either in individual intervals, or when data from a number of intervals are aggregated together) as time in the interval elapses.

How can this simple, but striking, example of temporal control be explained? Animals come to behave quite differently at some early time in the interval (A) than they do at a later time (B), and there is an obvious parallel between the different behavior at the different times A and B and the different behavior that would be observed if A and B were values on an exteroceptive stimulus dimension, for example, color. So, for example, if responding was extinguished in the presence of a green light (A) but reinforced in the presence of a red light (B), the different behavior in the presence of A and B would be regarded as a simple example of discrimination learning about the stimulus dimension of color. On FI, responses early in the interval (A) are not reinforced, or are followed by reinforcement only with long delays, whereas responses later in the interval (B) are reinforced, or followed by reinforcement with short delays, but regarding A and B as different values along some stimulus continuum in the same way that red and green are raises the problem of whether time can be considered as a stimulus, a question that has caused, and continues to cause, theoretical difficulties.

One might regard the temporal property of an event as simply another sort of property, like size, color, associated sounds, and so forth, but the questions arise of how this temporal property could be measured, and of what the ''receptor organ'' for temporal sensitivity might be. One might hypothesize that such an organ for time perception really exists in the form of some sort of internal clock that a behaving organism can have access to. According to this hypothesis, in our example above, A and B simply give rise to different, and discriminable, ''readings'' of this internal clock, so the behavior on FI is explained in the same way as other discriminations: The animal learns that responding in the presence of one stimulus is reinforced, and responding in the presence of another stimulus is not. However, the stimulus referred to here is internal, so if explanations in terms of such

*Published in Journal of the Experimental Analysis of Behavior (2006), vol. 85, n°1, pp. 125-142*
*DOI: 10.1901/jeab.2006.85.04*
*Status : Postprint (Author's version)*

internal events are regarded as undesirable, then some alternative must be found. In our example above, it seems impossible for animals to respond the way they do on FI without *something* being different about time periods A and B. As we shall discuss in more detail later, a number of accounts of animal timing in the behavior-analytic tradition have wrestled with just what the difference might be if time itself cannot be regarded as a simple stimulus dimension processed by an internal mechanism.

## PART 1: OPERANT METHODOLOGIES AND THEIR USE IN ANIMAL TIMING RESEARCH

The first major part of the article is divided into two main sections. The first of these discusses the development of operant methodology by Skinner, describing in particular procedures introduced in *The Behavior of Organisms* (Skinner, 1938) and *Schedules of Reinforcement* (Ferster & Skinner, 1957). The second section reviews developments of operant methodologies that came after *Schedules of Reinforcement*, in particular, changes from the 1970s up to the present, which have established a temporal ‘‘animal psychophysics.’’

### THE DEVELOPMENT OF OPERANT METHODS BY SKINNER AND COLLEAGUES

For a contemporary reader who is willing to make the little effort needed to master its now unfamiliar terminology, *The Behavior of Organisms* (Skinner, 1938) is a veritable treasure trove of methodological innovation. Chapter 4 introduces the technique of *periodic reconditioning*, which we now know as the FI schedule. Although FI schedules and their variants now are used extensively to study temporal control in animals, in 1938 Skinner's focus was largely, although not exclusively, on the response rate that such schedules produced and the factors that affected response rate, rather than the pattern of responding during FI intervals. The famous ‘‘scalloped’’ pattern of responding, familiar to us from *Schedules of Reinforcement* (Ferster & Skinner, 1957), appears in Figure 30 (p. 121) of *The Behavior of Organisms* as a ‘‘third-order deviation’’ from a constant response rate, and although it receives some theoretical discussion (which we will address in another section of this article), there is little experimental analysis of the response patterning the schedule produces within intervals. Response rate, in contrast, is treated extensively. One figure shows response rates from rats on FI values of 3, 6, 9, and 12 min, and a whole experiment (p. 127 ff.) is devoted to what would these days be regarded as a quantitative analysis of response rate, with rats receiving FI values from 3 to 9 min, and their resulting response rates plotted against FI value (Figure 33, p. 128). To the contemporary reader, the figure bears a striking resemblance to those common in post-1970 articles on the quantitative analysis of performance on various schedules of reinforcement. Ironically, the question of absolute response rate on FI, and schedules that involve temporal regulation in general, has received little attention in modern research where interest has been dominated by issues of temporal control (i.e., ‘‘when’’ to respond, rather than ‘‘how much’’), although some exceptions exist (e.g., Kirkpatrick, 2002; Machado, 1997). In other work using simple FI schedules, Skinner (1938, p. 129) presents data on transitions from FI 9 min to FI 3 min, and once again, transition from one schedule value to another has been a relatively neglected issue in modern research(but see Lejeune, Ferrara, Simons, & Wearden, 1997; Wynne & Staddon, 1988; Wynne, Staddon, & Delius, 1996).

In the 1938 book, Skinner used FI as a baseline schedule to which other contingencies could be added, or even subtracted. In one study, he reports the effects of adding delays of reinforcement (2 to 8 s) to an FI (e.g., Figure 40, p. 141), with the consequent effects of decreases in response rate. Another study (p. 152) presents data from an experiment adding a punishment contingency, in the form of a ‘‘slap’’ delivered by an upward movement of the lever. FI schedules also form the basis for the invention of two procedures that were to play a large role in our understanding of schedule control only 30 or 40 years later. In the first, ‘‘negative correlation of response and reinforcement’’ (p. 160 ff.), Skinner considers ‘‘the possibility that ‘not-responding’ may be reinforced . . .’’ (p. 161), and invents what we now would call ‘‘differential-reinforcement-of-other-behavior: DRO,’’ with the DRO contingency requiring that responding should be absent for 15 s before the reinforcer is delivered. This ‘‘negative correlation’’ between responding and reinforcement (a terminology that prefigures that of Baum, 1973) decreased response rate markedly (Figure 51, p. 162), and DRO was later used as a temporal differentiation procedure to study ‘‘pure timing’’ in animals (Zeiler, 1985). On the very next page, Skinner reports the invention of what we now would call the fixed-time (FT) schedule by removing the response requirement for reinforcement, a situation very similar to Pavlov's periodic conditioning. Over 9 days of exposure to FT 6 min, response rate declined markedly (albeit not to zero), with responding recovering quickly when the FI contingency was restored (Figure 52, p. 164).

As well as developing the FI schedule and variants, Skinner, in his 1938 publication, also developed methods for ‘‘differentiation of a response’’ (chap. 8, pp. 308-340). The first part of this chapter discusses the differentiation of response force, in which different force requirements are imposed for reinforcer delivery, but the part that concerns the present article is rather Skinner's work on differentiation of response duration, what we would now call ‘ ‘ differential-reinforcement-of-response-duration: DRRD.’’ Skinner first shows that durations of 4 and 5 s can be acquired by rats (Figure 112), then progresses in some rats to longer time requirements, reporting eventually successful performance but also the persistence (particularly at the start of the daily session) of shortduration responses not controlled by the reinforcement contingency. Difficulties in obtaining temporal differentiation of responses of very long duration, as well as the persistence of responses with short duration or interresponse times (IRTs) on schedules designed to reinforce longer durations or IRTs are, of course, results obtained in more recent studies (e.g., Kuch, 1974; Lejeune & Richelle, 1982; Platt & Scott, 1981; Staddon, 1965).

*Schedules of Reinforcement* (Ferster & Skinner, 1957) deepens the description of performance on many of the schedules of reinforcement invented by Skinner in his 1938 book. The long section on FI (chap. 5, pp. 133-325) provides many examples of behavior under such schedules (more than 350 figures, some containing examples of behavior from several different conditions). Limitation of space permits us to mention but a few of the many important results. Almost the first thing described is the transition from a schedule in which each response is reinforced (CRF), to FI (Figure 117). The acquisition of FI after original operant learning is another issue that not only has been neglected in terms of experimental study, but one that has received little if any theoretical analysis until Machado's model published in 1997. Machado used material from *Schedules of Reinforcement* to evaluate his model of timing, discussed later (see also Machado & Cevik, 1998). Further work in the chapter used FI schedules with various sorts of ''timeouts'' imposed after reinforcer delivery, and the work reported in another section employed an imposed ''clock.'' The method typically used with pigeons involved the presentation of a dark ''slit'' on the pigeon response key, where the size of the slit is correlated with elapsed time in the interval, thus acting as an external clock. Control by this external clock was established rapidly, and temporal control under these conditions was very precise, with responding confined to the period just before reinforcer delivery (e.g., Figure 213, p. 269). Control by the clock was tested by running the clock in conditions in which the reinforcer was not delivered, although the clock continued to cycle as in the previous FI condition, and the scalloped pattern of responding persisted for long periods in accordance with the setting of the clock previously used. A rather similar methodological innovation was the imposition of a counter (a projected stimulus the dimensions of which depended on the number of responses emitted) on FI. While a large amount of space in *Schedules of Reinforcement* was devoted to description of the effects of these manipulations, later research has rarely used them. However, a methodological innovation that has become commonly used was the *differential reinforcement of response rate*.

Chapter 9 of *Schedules of Reinforcement* deals with response rate control, and Ferster and Skinner distinguished two contingencies allowing for such control. The first, labeled ''differential reinforcement of high rates'' (DRH) specifies high response rates that should occur, for example over *n* responses, before reinforcer delivery. The second contingency, which has been important in the study of animal timing, was labeled ''differential reinforcement of low rates'' (DRL), and specified a low rate of responding as the requirement for reinforcer delivery. In this case, the ''rate [of response] at reinforcement'' is defined as the ''reciprocal of the Inter-Response-Time (IRT) that precedes a reinforced response'' (Ferster & Skinner, 1957, p. 459).

Given the later importance of DRL and related schedules in the study of animal timing, it is perhaps ironic that Ferster and Skinner generally regarded DRL not in terms of temporal differentiation of responding, but as a *procedure* that might be combined with other operant schedules to modulate response rate. For example, a single DRL might be added to an FI contingency: ''. . . in FI5drl6 a response is reinforced approximately every 5 minutes but only when it follows the preceding response by at least 6 seconds'' (Ferster & Skinner, 1957, p. 459). Consistent with this general position, the definition of DRL in the glossary at the end of *Schedules of Reinforcement* is couched in terms of response *rate* and not in terms of *time* between response units: that is, ''Reinforcement occurs only when the rate is below some specified value.''

The 43 pages devoted to DRL in *Schedules of Reinforcement* provide multiple cases of response-rate modulation on a variety of schedules by addition of a DRL contingency. One interesting variant using a variable-interval (VI) schedule was ''DRL with pacing,'' where a lower, but also an upper, limit was assigned to the DRL component, what in modern terms would be called a ''limited hold'' contingency. In all the cases discussed, the DRL contingency was limited to a single IRT, and not a series of IRTs. The case of a ''pure'' DRL schedule, in which only the ''rate'' (IRT) specification is in force, was not discussed.

The methodological fecundity of Skinner's work, particularly that represented in *The Behavior of Organisms*, should be obvious from the brief review above. From the point of view of animal timing alone, many novel methods were developed by Skinner, and much data presented (particularly in *Schedules of Reinforcement),* although some issues explored by Skinner, and by Ferster and Skinner, have received little attention since (e.g., external clocks, timeout effects). In addition, something that strikes a contemporary reader is that procedures that are considered these days to be keys to understanding temporal control in animals are, in both *The Behavior of Organisms* and *Schedules of Reinforcement*, but particularly the former, mainly discussed in terms of their effects on *response rate,* so issues relating to temporal control, which seem to arise so strikingly from the data, rarely receive the discussion they seem to merit. More modern developments of operant methods have used techniques initially invented by Skinner more or less exclusively for the study of temporal control in animals, with issues of response rate on schedules that have temporal periodicities (like FI) being almost completely neglected. We turn next to some more recent developments in operant methodologies for the study of animal timing.

## THE EVOLUTION OF OPERANT METHODS: 1950S TO THE PRESENT

One major feature of developments in operant techniques for the study of time during the second half of the twentieth century has been their application to animal psychophysics. Since the nineteenth century, psychophysics has explored time perception in humans by using classical procedures, involving the discrimination, production, reproduction, or comparison of durations. Two principal issues arose. One concerned the relation between mean measures of time judgement and the real-time values of presented events: for example, how did mean ‘‘estimates’’ of time (assessed by various methods) change as the duration of stimuli to be estimated was varied? One possibility is a linear relation between mean and real time, but logarithmic and power relations also were sometimes found (e.g., Eisler, 1976). The other issue concerned relations between variability of time judgements and the mean, in particular the question of whether or not time perception conformed to Weber's law. Weber's law in timing can be assessed in various ways, but one technique is to plot the relation between the standard deviation of time judgements and the mean, with simple proportionality being found if Weber's law holds. Another method is to construct a Weber fraction (i.e., dividing the standard deviation by the mean to produce a coefficient of variation): This Weber fraction is a measure of the relative sensitivity of timing, and if Weber's Law holds, it should remain constant with changes in the absolute values of durations timed. Operant methods offered the possibility of extending time psychophysics studies to animal subjects. Chapters in two edited books published in the 1970s (Schoenfeld, 1970; Zeiler & Harzem, 1979) were particularly influential in developing this area.

The relevant chapters in Schoenfeld's book, *The Theory of Reinforcement Schedules*, were representative of the behavior-analytic approach to schedule performance as it had developed in the 1960s, and mostly reflected a Skinnerian position quite clearly. Two chapters were devoted to timing behavior. The first, entitled ‘‘Reinforcement Schedules and Psychophysical Judgments’’ (Catania, 1970) offered, besides a parametric study of pigeons' behavior on a differential-reinforcement-of-long-latencies schedule (DRLL), several figures presenting summary data from animal and human timing experiments, some of them long predating Skinner's invention of operant methods (see Figure 1-11, p. 32). Catania's study of DRLL used pigeons and reinforced response

*Published in Journal of the Experimental Analysis of Behavior (2006), vol. 85, n°1, pp. 125-142*
*DOI: 10.1901/jeab.2006.85.04*
*Status : Postprint (Author's version)*

latencies ranging between 0.60 and 48 s, and found that power functions with a fractional exponent could be fitted to the relation between the mean response latency and the imposed time requirement, in fact similar power functions as had been found to fit previous results from humans.

The other influential chapter was authored by Dews (1970) and titled ''The Theory of Fixed-Interval Responding.'' Dews emphasized two important results. One was that the scalloped pattern of increasing response rate throughout the FI interval survived interruptions in the pattern of responding occasioned by stimulus changes. This finding effectively ruled out the notion that the FI response pattern was due to some simple sort of chainlike cueing, where the rate of response at one time period acted as a cue for responding in the next one. The second was Dews' plot of response rate during quarters of different FI values as a function of the rate at the end of the interval. Dews showed (Figure 2-2) that, when this measure was plotted against quarters of the elapsed time in the interval, results superposed across a 100-fold range of FI values, from FI 30 s to FI 3,000 s. This was a very early example of the ''proportional timing'' so important for the later development of Scalar Expectancy Theory (SET; Gibbon, 1977; Gibbon, Church, & Meck, 1984).

Another important contribution to the study of temporal psychophysics in animals was written by Platt (1979) in the book edited by Zeiler and Harzem (1979). In that chapter, Platt explicitly linked behavior on temporal differentiation schedules to the psychophysics of time. He reviewed data from DRL, DRLL (Catania's 1970 data), DRRD (invented by Skinner, 1938), and differential reinforcement of ratio duration and latency. He concluded that Weber's law and the power law appeared to hold when small time requirements for reinforcement were imposed, whereas with longer imposed temporal constraints, both laws appeared to fail. However, Platt suggested that such failures should not be considered as evidence against the laws, but as indices of interference by other processes; for example, those minimizing response duration, response cost, or base duration (i.e., the mean response duration in the absence of any timing requirement). In general, Platt considered that temporal differentiation schedules were not appropriate tools for the study of animal timing processes, largely because the animal's behavior did not always come into contact with the experimenter's reinforcement contingencies, particularly when imposed time requirements were large. In fact, Platt's suggestion of adding ''other'' processes to a basic mechanism in order to account for deviations from the simple mechanism's predictions has been common in recent developments of the SET model (see Wearden, 1999, 2004, for discussion).

Stubbs (1979), in the same book, also presented data obtained with animal analogues of the classical psychophysical procedures. In an echo of Platt, Stubbs also questioned whether reinforcement schedules, because of their inherent complexity, were well suited for the study of temporal discrimination. In spite of these reservations, however, discrimination methods based on operant procedures were later designed. Stubbs distinguished between four categories of procedures: procedures involving reinforcement schedules, discrimination procedures deriving from reinforcement schedules, psychophysicaltrials procedures, and free-operant psychophysical procedures. The omnipresence of operant schedules in three of these categories testifies again to Skinner's immense influence on the study of animal timing at the methodological level.

Experimental techniques using operant methods have been used more recently to test predictions from different timing models, most notably the most influential account of animal timing, SET. SET is a cognitive account of animal timing that explains timed behavior in terms of an interaction of internal clock, memory, and decision processes. A pacemaker-accumulator internal clock provides ''raw'' representations of duration, and ''important times'' (e.g., the time of reinforcement on FI) are stored in a reference memory. Timed behavior arises from decision processes that compare elapsed time with samples from reference memory. For example, to simplify slightly, SET would explain FI performance as follows. As the interval elapses, ''ticks'' from the pacemaker accumulate, and when the reinforcer is delivered at *t* s, the number of ticks accumulated is stored in reference memory. Responding is generated by a comparison of currently elapsed time in the interval and a sample drawn from the reference memory. The current accumulator reading is compared with the number of ticks representing the time of reinforcement, and if these two are ''close enough,'' according to a mathematically specified decision rule, then the animal begins to respond (see Gibbon et al., 1984, for a more formal account).

SET accommodated and formalized behavioral characteristics present in previous empirical data (see Gibbon, 1977, for numerous examples) and provided an account of animal timing in which overt behavior was merely an indication of the putative internal mechanics of the timing model. SET proposes that timed behavior exhibits certain empirical characteristics. One of the most important of these is ''relative timing,'' exemplified in terms both of mean behavior measures and measures of the variability of behavior. For example, according to SET, the time at which responding emerges on an FI schedule is a proportion of the FI value, not an absolutely fixed time. In addition, measures of timed behavior exhibit a Weber-like variance property, where their standard deviation varies as a constant fraction of the mean. As noted above, Dews (1970) provided an early example of such relative timing as represented by the superposition of response rate in FI, when measures of behavior from very different FI values were superposed on the same relative scale. Superposition later was considered as one of the hallmarks of SET, that is, of response timing obeying Weber's law (Gibbon, 1977). In an article discussing the origins and development of SET, Gibbon (1991) mentions particularly the influence of the data from both Dews and Catania published in 1970, mentioned above.

Simple FI schedules and some FI variants also have been used to test SET. For example, Lejeune and Wearden (1991) fitted the left half of Gaussian curves to the averaged response rate versus elapsed time in the interval function derived from a range of animal species under FI. This article, comparing animal species ranging from a freshwater turtle to cats, showed that the scalar property of variance measured by the coefficient of variation (CV) of the Gaussian curves generally held over a range of durations, but that CVs tended to increase as the FI value became very large. It also highlighted species-specific sensitivity to time, as CV values, a kind of index of temporal sensitivity, differed considerably from one species to another. In other respects, however, the behavior of different species on FI seemed strikingly similar, echoing Skinner's famous question (Skinner, 1956) ''which is which?'' Skinner posited that schedules of reinforcement could ''transcend'' or ''erase'' species-specific differences and yield performance (such as cumulative records on FI schedules) that did not differ in essentials from one species to another. Although species differences in the temporal control of behavior do occur (e.g., Lejeune & Wearden, 1991; Lowe & Harzem, 1977), some aspects of timing

*Published in Journal of the Experimental Analysis of Behavior (2006), vol. 85, n°1, pp. 125-142*
*DOI: 10.1901/jeab.2006.85.04*
*Status : Postprint (Author's version)*

do seem to have cross-species generality, supporting Skinner's position, and such generality even may extend to humans (e.g., Lejeune, 1990; Richelle, 1968; Richelle & Lejeune, 1984; Richelle, Lejeune, Perikel, & Fery, 1985; Wearden, 1991).

In a further example, data from mixed-FI schedules recently have been analyzed to test competing contemporary accounts of animal timing, such as SET versus the *Behavioral Theory of Timing* (BeT; Killeen & Fetterman, 1988) and the *Learning to Time* model (LeT; Machado, 1997), as discussed by Whitaker, Lowe, and Wearden, (2003; see also Leak & Gibbon, 1995). In a two-valued mixed-FI schedule, the reinforcer is delivered for responses at two different times after the previous reinforcer delivery, but only one reinforcer can be obtained in each individual interval, and nothing signals which FI value is in force in any particular interval. Ferster and Skinner (1957) described data from large-valued mixed FI FI in pigeons (mixed FI 330 s FI 30 s, pp. 597-599; FI 5 min FI 1 min, pp. 599605; and FI 20 min FI 4 min, pp. 613-615) and presented cumulative records of data from individual pigeons, illustrative of the development of performance, in one case over 400 hours (Figure 755, mixed FI 5 min FI 1 min). The detailed description repeatedly mentions a ''priming'' phenomenon when the longer-valued FI is entered after the shorter one, that is, a sustained response rate followed by a ''falling-off into a curvature appropriate to the longer interval'' (p. 597). These primings probably represent, in contemporary terms, a response-rate distribution with one peak located at about the shorter FI value of the mixed-FI schedule, as found in a recent analysis by Whitaker et al. (2003; see also Leak & Gibbon,1995).

The Peak Interval (PI) procedure, which mixes FI and extinction (Catania, 1970; Roberts, 1981), has been strongly associated with tests of SET (Church, 1984; Gibbon et al., 1984; Roberts, 1981). To change FI into a PI task, three alterations are made. First, trials are signaled by an exteroceptive stimulus, and separated by variable-duration intertrial-intervals. Second, some of the FI trials last at least twice the duration of the FI. Third, these so-called ''peak trials'' end without reinforcer delivery (so are extinction trials). Response rate versus elapsed time functions recorded on peak trials usually follow a Gaussian shape and display mean accuracy (i.e., the peak of the curve is at the normal time of reinforcement) and a Weber-like variance property (so the spread of the curve varies proportionally with the time of reinforcement), in agreement with SET. Besides analysis of response rate versus elapsed-time functions aggregated over a large number of intervals, data from individual peak trials allow exploration of the detailed mechanics of SET (e.g., Buhusi & Meck, 2000; Church, Meck, & Gibbon, 1994).

Temporal differentiation schedules, such as DRL or DRRD, have been used recently for testing predictions of SET. IRT or responseduration distributions have been fitted with Gaussian functions that yielded peak location values and variance properties in accord with the requirements of SET (Jasselette, Lejeune, & Wearden, 1990; Lejeune, Huynen, & Ferrara, 2000). These data were, however, obtained using operants different from the classical key peck or lever press; for example, a ''perching'' response in pigeons and a ''platform'' response for DRRD in small rodents. The DRRD schedule bears a procedural resemblance to the method of interval production used in timing research in humans, which also yields data in agreement with SET if chronometric counting is prevented (Wearden & McShane, 1988; see also Wearden, 2003).

Overall, it can be seen that experimental methods based on schedules of reinforcement developed by Skinner (1938) and Ferster and Skinner (1957) have been central to the study of animal timing and that without such methods the immense progress that this field of research has made would probably never have occurred.

Although we have concentrated on the development of operant methods, derived from work by Skinner himself, some brief mention should be made of more recent suggested connections between timing in operant and Pavlovian learning. Some procedures like autoshaping (Brown & Jenkins, 1968; see also Gibbon & Balsam, 1981, Hearst & Jenkins, 1974, Schwartz & Gamzu, 1977, for example) have eroded the distinction between Pavlovian and operant behavior, emphasizing the interaction between classical and operant learning processes, and underscoring the fact that Pavlovian control may play a role in operant procedures (for recent data, see, e.g., Brown, Hemmes, Cabeza de Vaca, & Pagano, 1993; Drew, Zupan, Cooke, Couvillon, & Balsam, 2005; Kirkpatrick & Church, 2000). Some recent theoretical arguments in addition suggest that timing processes, like those usually studied by the operant methods described above, play a critical role in all types of Pavlovian conditioning (Gallistel & Gibbon, 2000; Savastano & Miller, 1998), and integrated models of animals' timing in both operant and Pavlovian procedures recently have been developed (see Kirkpatrick & Church, 2004, for example). The wheel thus seems to have come full circle, from Pavlovian inhibition of delay, through the development of animal timing procedures inspired by Skinner's operant methods, back to a more integrated view of temporal control in all situations in which animals learn.

# PART 2: BEHAVIOR-ANALYTIC APPROACHES TO ANIMAL TIMING

The second major part of the present article also is divided into two different sections. The first one discusses explanations of temporal control in animals provided by Skinner in *The Behavior of Organisms.* The second section discusses some more recent explanations of animal timing that have followed, or tried to follow, the behavior-analytic principle of explanation with no, or minimal, reference to internal processes.

## SKINNER'S EXPLANATION OF ANIMAL TIMING

In *The Behavior of Organisms* (Skinner, 1938), Skinner devoted some space, particularly in chapter 7 (pp. 263-307) entitled ‘‘Temporal Discrimination of the Stimulus,'' to considerations of the role played by time in both Pavlovian and operant learning processes. Skinner clearly thought that time could not be treated simply like some other stimulus dimensions; for example, ‘‘the problem is how time as a dimension of nature enters into discriminative behavior'' (p. 263). Skinner notes that ‘‘time is frequently spoken of as a stimulus,'' particularly by Pavlov, whose long- delay method gave rise to the so-called inhibition of delay Skinner was discussing in this section of *The Behavior of Organisms.* But, he concludes, ‘‘Time has not the proper dimensions of a stimulus'' (p. 269). In contrast, Skinner also writes that ‘‘Time appears as a single property of duration, comparable with intensity, wavelength, and so on'' (p. 269).

For the contemporary reader, the feature of responding on FI schedules that is most striking, and most in need of explanation, is the temporally differentiated pattern of responding within the interval, what Skinner (1938) calls the ''third-order deviation,'' but in *The Behavior of Organisms* the explanation of this effect (although frequently referred to as a ''temporal discrimination'') receives little space. Skinner makes a number of observations. He asks the question: "why does the rat not simply learn to wait until the time of reinforcement [on FI]?'' (p. 271), and answers this by arguing that temporally different points in a stimulus may be harder to discriminate from one another than two distinct external stimuli (the example he gives is *light-on* versus *light-off),* but another feature that causes discriminative problems for the behaving animal is the fact that the duration of an event elapses continuously (pp. 272-273).

Skinner (1938) discusses two possible mechanisms for the establishment of temporal control within the interval. One is ''temporal discrimination of the preceding reinforcement,'' so ''the reflex in response to the lever immediately after receipt of a pellet is weakened because it is never reinforced at that time'' (p. 125). Another idea used by Skinner to explain temporal control was a ''second temporal discrimination of Type R'' and concerns the ''temporal discrimination of the preceding response,'' that is, ''the interval of inactivity immediately preceding the reinforced response'' (p. 274). This happens because ''if there is any local variation in rate, it is more likely that a reinforced response will be preceded by a *longer* period of inactivity'' (p. 274). The consequence of this discrimination is to ''strengthen responses following long intervals of inactivity'' (p. 275) as the reinforcer is dispensed as response rate weakens at the end of the interval. This position is reminiscent of a number of more modern ideas about how interval schedules reinforce patterns of responding. On any interval schedule, responses following periods of nonresponding have higher probabilities of reinforcement than those following responses, because the timer ''setting-up'' the reinforcer is likely to have ''timed-out'' during the period of inactivity and thus arranging for the next response to be reinforced. Thus VI schedules differentially reinforce long IRTs rather than shorter ones, but the question of whether this differential reinforcement is the sole explanation of performance on such schedules remains difficult to judge even now (e.g., Wearden & Clark, 1988). Likewise, Skinner appears to suggest a similar process on FI, some kind of alternation of response periods and periods of other behavior, which the reinforcer delivery organizes into a pause-respond pattern in a manner similar to the recent suggestions of Dragoi et al. (2003).

The obvious question that arises for a contemporary reader is what mechanism Skinner proposed in 1938 to account for the development of temporal discriminations. That is, what is the mechanism by which ''the organism may begin to distinguish between the stimulus momentarily at [one] point and the same stimulus momentarily at another point by reacting differently to the two . . . a temporal discrimination, as the term will be used here'' (p. 265). Although he sometimes refers to ''the receipt and ingestion of food'' (p. 271) as a possible basis for discrimination, this suggestion is not developed, and Skinner provides no ''mechanism'' for temporal discrimination, that is, he does not attribute the animal's sensitivity to time to an internal clock, or to any other process. However, this position is consistent with the treatment provided in *The Behavior of Organisms* of nontemporal discriminations: The aim of the exercise is to try to understand the ways that stimulus dimensions (e.g., color, light, or sound intensity) control behavior, not to uncover (or even discuss) the

*Published in Journal of the Experimental Analysis of Behavior (2006), vol. 85, n°1, pp. 125-142*
*DOI: 10.1901/jeab.2006.85.04*
*Status : Postprint (Author's version)*

mechanisms of perception of different sorts of stimuli.

### MODEM ''BEHAVIORAL'' ACCOUNTS OF ANIMAL TIMING

In this section, we will review fairly recent models of animal timing that can be traced back to Skinner's work, and the radical behaviorist theoretical position he advocated, in particular his stance that behavior should not be explained in terms of internal processes. This view has led to three recent behavioral models of timing, namely Killeen and Fetterman's (1988) BeT, Machado's (1997 *LeT*, and the *Adaptive Timer Model* (ATM) of Dragoi et al. (2003). All three theories attempt to account for aspects of animal timing without resorting to the cognitive apparatus (internal clock, memory, and decision processes) of SET.

The authors of these three theories take care to distinguish their approaches from SET and other accounts of timing that rely on internal processes, and themselves define their approach as being behavioral. For example, as Killeen and Fetterman (1988) write, ''This behavioral theory of timing constitutes a formalization of the view that behavior is the mediator of temporal control .... Other explanations of the timing process have implicated internal operations and comparisons as the basis of animals' perception of time (e.g., Gibbon & Allan, 1984). We do not talk about the perception of time or subjective scales of it. . . but rather of simple conditioned discriminations'' (p. 274). Similarly, Machado (1997) argues that LeT ''is a behavioral, not a cognitive, connectionist, or neurophysiological model . . . because it emphasises the role of the behavior of the animal and its interactions with the environment in the development of temporal control'' (p. 242). Concerning ATM, Dragoi et al. (2003) assert that ''the major facts of interval timing can be explained without reference to an internal clock, time scale, or explicit comparison process … We demonstrate temporal discrimination in a model that has no pacemaker or fixed internal scale for time'' (p. 128).

Two other recent theories, the *Multiple Time Scales* model of Staddon and Higa (1999) and its dynamic derivate, the *Tuned Trace* model of Staddon, Chelaru, and Higa (2002), which also have been advanced as competitors to SET, are not behavioral theories in the same sense as the others mentioned above, as they essentially replace the internal clock of SET by memory decay, so still measure time by some essentially nonbehavioral process, and these accounts will not be discussed further here.

## SOME PRECURSORS OF BEHAVIORAL MODELS OF TIMING

Although the idea of behavior-mediated timing used in some recent models was not developed by Skinner himself, a paper published in 1948 provided a precursor of this idea. This paper entitled ''Superstition in the Pigeon'' described behavior of pigeons on a FT 15-s schedule, where food is provided every 15 s independently of the animal's behavior. Some of the pigeons developed stereotyped activities, such as pecking the floor or circling the cage, that supposedly were related to phylogenetic or ontogenetic factors, such as experimental history. These behaviors were labeled ''superstitious'' because they were not instrumental to the delivery of the reinforcer but appeared to be strengthened adventitiously as they were occasionally reinforced by food. These adventitiously reinforced responses eventually filled the time between food deliveries.

The idea of a possible contribution of usually unmeasured behavior to timing of measured operants developed from data published from the 1950s onwards. One of the first papers reporting the occurrence of so-called series or ‘‘chains’’ of ‘‘collateral’’ behavior different from the operant on DRL was published by Wilson and Keller (1953). As these chains of behavior occurred during the IRTs, early interpretations of DRL performance suggested that animals simply discriminated sequences of their own actions instead of measuring time (the same hypothesis applied to behavior under FI was discussed by Anger, 1963 and Dews, 1962). This ‘‘chaining’’ hypothesis supposed that each collateral behavior directly induces the next one, up to the reinforced and measured operant response, just as happens in a row of falling dominos. Temporal regulation was thus ‘‘mediated’’ by chains of the organism's own actions, and these chains (that might also be considered as a kind of ‘‘behavioral clock’’) offered a convenient way of explaining temporally regulated behavior without positing any internal timing device.

After Wilson and Keller's (1953) publication, several papers on DRL reported chains of collateral activities made of different or identical components that were thought to mediate duration and could be used as a behavioral clock. However, doubts as to the exact role of these behavior chains arose and these stimulated renewed experimentation. Anger (1963) noted that the observation of so-called mediating behavior does not prove that this behavior is crucial for temporal regulation of operant behavior (see also Nevin & Berryman, 1963). To test the idea that the temporal regulation of measured operants was mediated by other activities, potential collateral chains were interrupted by blackouts (Dews, 1962, 1965), disrupted (grid nibbling in rats was suppressed by placing a panel over the grid floor, Laties, Weiss, & Weiss, 1969), reduced (pigeons were placed in small cages that restrained collateral activities, Frank & Staddon, 1974; Glazer & Singh, 1971), favored (wood blocks were provided to rats for nibbling or supplementary response keys provided to pigeons, Laties et al., 1969; Zuriff, 1969) or even reinforced (Segal-Rechtschaffen, 1963), and all data converged to show that collateral activities, when present, might improve the temporal regulation of behavior. However, the research also suggested that these activities did not seem to be necessary and sufficient for temporal regulation of measured operants to occur.

As well as the possibility of collateral behavior playing a role on DRL-like schedules, behavior occurring during the postreinforcement pause (the period before emission of the first operant response in the interval) under FI schedules also aroused interest. Staddon and Simmelhag (1971) reconsidered the relation between operant and other classes of behavior (natural or experimentally induced), and showed that collateral activities in FI appeared and were maintained for reasons other than response-reinforcer contiguity, thereby questioning Skinner's superstitious or adventitious-reinforcement hypothesis described above. Staddon and Simmelhag labeled these collateral behaviors as ‘‘adjunctive’’ or ‘‘schedule induced’’ and classified them into different categories, according to their time of occurrence. ‘‘Interim’’ activities, such as running, preening, or wing flapping in pigeons, occurred early in the interval and were thus temporally remote from reinforcer delivery, whereas ‘‘terminal’’ activities, such as pecking the walls or exploration of the food area, occurred towards the end of the interval, thus were closer to reinforcer delivery, and better candidates for an explanation in terms of adventitious reinforcement. ‘‘Facultative’’ activities were located in between. According to Staddon (1977), these facultative activities are not schedule induced. The origin and functions of collateral or schedule-induced behavior were discussed in several publications, among which are Falk (1977), chapter 7 in Richelle and Lejeune (1980), Roper (1981) and Staddon (1977).

It can be seen that ideas deriving from Skinner's (1948) superstition experiment contributed greatly to behavior-analytic views of how behavior on temporally regulated or constrained schedules was controlled. Whether or not superstitious behavior was maintained by contiguity with the reinforcer, the existence of such behavior offered a potential solution to the time problem discussed at the start of this article. Our hypothetical time periods A and B must be distinguished in some way for temporal control of measured behavior to develop as it does, and one way is to have discriminably different collateral/adjunctive behaviors occurring at times A and B. According to this view, on temporally constrained schedules, animals are sensitive to something other than the passage of time (albeit something that must be correlated with elapsed time), and their behavior shows adjustment to schedule conditions imposing temporal periodicities and constraints only because of underlying sequences of adjunctive behavior. The animal is not directly sensitive to time at all, according to this view, but merely uses, in some way, usually unmeasured behavior to control the operant response. This sort of idea was most fully developed theoretically by Killeen and Fetterman (1988) in what has become the most influential behavioral model of animal timing, and that will be discussed next.

## KILLEEN AND FETTERMAN'S BEHAVIORAL THEORY OF TIMING (BeT)

The *Behavioral Theory of Timing* (BeT) of Killeen and Fetterman (1988) may be considered as a blend of the cognitive idea of an internal timing device and the mediating-behavior hypothesis described above. BeT suggested that animals use adjunctive behavior as cues for the emission of the measured operant. However, whereas in the mediating-behavior hypothesis each collateral behavior was considered as the discriminative stimulus for the production of the next one, in BeT, transition between different adjunctive activities (the behavioral states) was controlled by pulses of a pacemaker, the rate of which depended on the rate of reinforcement in the experimental context. However, the possibility that the link between pacemaker pulses and state changes might be more complicated than the simple model specifies also was discussed. For example, the animal may stay in the same state for more than one pulse (Killeen & Fetterman, 1988), it may ‘‘mistakenly'' reenter a state correlated with an earlier adjunctive response, pulses may be ‘‘missed,'' or external stimuli may ‘‘pull'' the animal out of one state into another, so the exact relation between pacemaker activity and adjunctive behavior can be somewhat blurred.

For example, according to a later paper of Killeen and Fetterman (1993), it may happen that ‘‘A pulse from the (irregular) pacemaker might occur before the animal even has the chance to emit the behavior characteristic of that state… Thus, states are propensities to respond.... Because these hypothetical states are not the same as the observed classes of behavior, they will not be perfectly correlated with them. The states are driven by the pacemaker, and behavior follows suit as best it can'' (p. 413). The model thus ‘‘does not entail a ‘behavioral chain' in which one response is necessary for the next'' (p. 413). This redefinition of a state as an ‘‘hypothetical propensity'' introduces the idea of ''covert'' entities making up the ''classes of behavior,'' which departs from the purely behavioral framework and makes testing the theory by recording nonoperant activity produced between the schedule-defined responses somewhat problematical.

In its initial version, BeT predicted that systematic linear changes in the rate of adjunctive behavior should occur when the temporal criterion for reinforcement is changed, and that some degree of consistency between sequences of adjunctive behavior should be found. A few experiments have tried to record and analyze the behavior produced between successive measured operants. Lejeune, Cornet, Ferreira, and Wearden (1998) recorded the adjunctive behavior of gerbils that were reinforced with food for periods of platform residence according to a DRRD schedule, and outcomes for BeT were mixed. On the positive side, the rate of adjunctive activities varied linearly with reinforcement rate, as BeT predicts. The number and nature of adjunctive behaviors, however, were less consistent with the predictions of BeT. For example, adjunctive sequences were highly variable from one trial to the next, and some adjunctive activities seemed to be repeated within a sequence, thus causing potential problems of discrimination. In another experiment, rats and pigeons were videotaped on a discrete-trial temporal-discrimination task using spatially separate response devices. The analysis of correlations between behaviors recorded during the signals and subsequent categorization of durations as ''short'' or ''long'' showed that behavior during the signals was a better predictor of subsequent choice than elapsed time, in agreement with BeT. However, data from pigeons on a nonspatial version of the same task failed to support the behavioral-mediation hypothesis (Fetterman, Killeen, & Hall, 1998). Overall, therefore, attempts to test BeT by observation of adjunctive activities has produced results that do not seem completely consistent with BeT's predictions.

## MACHADO'S LEARNING TO TIME MODEL (LeT)

As in the original version of BeT, this model derives temporal regulation of the operant response from a sequence of behavioral states (Machado, 1997). The series of states is assumed to subserve the measure of time; however, transitions from one state to the next do not depend on a pacemaker, as in BeT. Rather, the model assumes that after a time marker (defined as a significant biological event or a reliable predictor of that event) a set of behavioral states is serially activated and that operant response rate at each moment in the interval depends on the level of ''activation'' or ''arousal'' of the state and the strength of its ''coupling'' or ''association'' to the operant response. To explain activation, Machado uses the analogy of a cascade of water through connected compartments where the amount of water represents the degree of activation of a state, the spread of activation across states being determined by the size of the hole drilled at the bottom of each reservoir (see Machado's Figure 2). So, for example, on a simple FI schedule, immediately after reinforcer delivery, the activation or arousal of the corresponding state (the first reservoir in the cascade) is maximal, whereas its coupling to the operant is low, due to the fact that the reinforcer is rarely if ever delivered when this state is active. Whereas in the initial version of BeT a state is used as a cue for operant responding, LeT suggests that responding depends both on the level of activation of a state and on the strength of its association with the operant, with the combination of activation and association being determined according to a multiplicative rule that determines response rate. In discussing the nature of the states, Machado refers to articles on adjunctive behavior such as Staddon and Simmelhag (1971), noting, however, that ''how best to conceptualize the different behaviors observed during the interreinforcement intervals remains an unsettled issue, but . . . only the relative invariance of the serial order of the behavioral states is critical'' (p. 242). This clearly implies that the states should be (a) observable, and (b) emitted in some sequence that should be detectable by observation. This model, which adds an associative component to BeT, can generate predictions about the acquisition of response timing (Machado & Cevik, 1998), whereas BeT and SET restrict their predictions to steadystate behavior.

LeT solves the timing problem discussed in the introduction by having different states active at times A and B, as well as having different couplings with the operant response for states active at times A and B. If responses occur during states active at A, then the nonreinforcement of such responses reduces the coupling between these states and the measured operant by means of an extinction like process. Responses occurring during states active at B, however, are followed by reinforcer delivery, so the states active at B increase their coupling with the measured operant. The result of this process is the temporal control normally observed on FI schedules, with little or no responding early in the interval (A) and responding later (B). According to LeT, however, the animal is not making any kind of judgement or comparison of A and B; the temporal control results from the combination of the succession of states and the automatic increase or decrease in coupling of states and responses depending on the reinforcement of responses in the presence of states.

## DRAGOI ET AL.'S ADAPTIVE TIMER MODEL (ATM)

Perhaps the most radical attempt to replace some kind of internal clock with a behavioral process was proposed by Dragoi et al. (2003) in a complex model that we can outline only briefly here. This account aimed to discover whether some aspects of timing behavior might be subtended by emergent properties of nontemporal learning processes. The model suggests that response timing on reinforcement schedules such as DRL or FI can emerge simply from elementary assumptions about response competition and arousal, that is, from a dynamic process without a time measuring device. The basic assumption of the model involves competition between reinforced R and all other behavior *O.* So, for example, temporal regulation of responses on DRL or FI depends on the organization of sequences of *O* behavior, followed by one or more *R* behaviors. The current strength of *R* or *O* depends on previous history and on a decay parameter that governs the frequency of alternation between *R* and *O*. The second assumption is that the value of this decay parameter is affected by the rate of reinforcement in the experimental situation, so rates of alternation between *R* and *O* are less frequent (i.e., longer sequences of each can occur) when reinforcement rates are lower. So, for example, a long FI that is associated with a low rate of reinforcement organizes longer consecutive sequences of *O* (constituting a postreinforcement pause) and *R* (constituting a postpause period of responding) than do shorter FIs. As well as the mechanism for controlling emission of *R* and *O* and the rate sensitive decay parameter, the model has other features, such as a process controlling response variation or added ''noise,'' which also plays an important role in determining output.

With appropriate choice of parameters, ATM can acquire spaced responding on DRL schedules and produces output that is sensitive to DRL value (e.g., Dragoi et al., 2003, Figures 6 and 7), and it also can acquire temporally differentiated patterns of responding on FI (Figure 12). However, the model encounters difficulties with some schedule conditions, discussed later.

The ATM model derives timed behavior from lower-level processes than previous models based on cognitive or behavioral clocks, but is more complex than it might appear at first sight, having response-competition mechanisms, parameters that vary with reinforcement rate (thus perhaps implicitly incorporating time into the system), and noise mechanisms needed for response stabilization. However, ATM fits well with the radical behaviorist tradition, as it bypasses cognitive hypotheses about the measuring of time. It also is a real time model that adds a ‘‘dynamic’’ dimension absent from BeT, SET, and the chaining hypothesis, so that predictions can be made about acquisition of response timing, and not only about steady-state performance.

## GENERAL COMMENTS ON ‘‘BEHAVIORAL’’ MODELS

How successful have the behavioral models of timing been? A complete discussion of this issue is beyond the scope of this article, but on the positive side, the behavioral models generate some predictions beyond the scope of SET. One such set of predictions concerns the learning of response timing, which can be accounted for by LeT and ATM, although not by SET in its current form.

Several papers published in the 1990s described data consistent with the BeT model (e.g., Bizo & White, 1994a, 1994b, 1995; Fetterman & Killeen, 1991; Killeen, Bizo, & Hall, 1999). However, conflicting results also have been reported (Beam, Killeen, Bizo, & Fetterman, 1998; Bizo & White, 1997). ‘‘Simultaneous’’ timing tasks, where the subjects must adapt to three different durations (short, intermediate, and long) yielded contrasting results, in one case congruent with SET (Leak & Gibbon, 1995), and in the other congruent with BeT (Fetterman & Killeen, 1995). Such a discrepancy might, however, be related to procedural differences; whereas Leak and Gibbon (1995) used a single key for two or three FI intervals, Fetterman and Killeen (1995) presented the short, medium, and long FI durations on spatially distinct response keys.

Another set of predictions involves reinforcement rate effects on the rate of the pacemaker of the internal clock. For SET, this rate is on average fixed, whereas for BeT, the pacemaker rate varies proportionally with the rate of reinforcement. Tests of this idea have met with varied success for both accounts. Mixed-FI schedules, where the timing of behavior in one component of the schedule can be measured while the rate of reinforcement overall in the experimental situation can be manipulated, were used to distinguish predictions of BeT from those of SET (Leak & Gibbon, 1995). According to BeT, the precision of timing of some constant duration should worsen (i.e., variability should increase) as reinforcement rate falls. Whitaker et al. (2003) found little support for this prediction from consideration of an extensive body of data obtained from mixed-FI schedules.

Manipulating the magnitude or the duration of the reinforcer also provided results apparently conflicting with BeT. A recent study of reinforcer magnitude effects on FI (Blomeley, Lowe, & Wearden, 2004) yielded data that appear the opposite of those predicted by BeT, although the results are not predicted by other models either. Other tests of the different models using the ‘‘time-left'' procedure and manipulations of motivation by unequal reinforcement durations in different components yielded data inconsistent with BeT (Gibbon & Fairhurst, 1994).

Finally, as mentioned above, measures of adjunctive behavior on a discrete-trial duration discrimination or a DRRD schedule only partly confirmed the predictions of BeT (Fetterman et al., 1998; Lejeune et al., 1998). Observation of considerable variability in sequences of adjunctive behavior also seems to directly contradict Machado's position that the serial order of states should be invariant (e.g., Machado, 1997), although the question of whether the adjunctive behavior sequences necessarily need to be invariant in behavioral models of timing is a complex one, discussed in Lejeune et al. (1998).

Mixed-FI schedules also are useful for testing predictions of Machado's LeT (1997). This theory deals with the vexed question of relative response rate on the two components of the mixed-FI schedule: If the mixed-FI schedule is constructed from two components, FI $a$ and FI $b$, where $a < b$, LeT's prediction is that the response rate at time $b$ should always be higher than at time $a$. The reason for this is that responses occurring during the states active at the shorter time $a$ will be both reinforced (when the reinforcer is delivered according to FI $a$) and extinguished (when FI $b$ is in force), whereas responses occurring in states active at the time of FI $b$ can only be reinforced (as they are not activated at time $a$). As a consequence, the coupling is higher between states active at $b$ and the response than states active at $a$, with consequent higher response rates at $b$. Whitaker et al. (2003) found instances of higher response rates at $b$ than $a$, but the conjecture that this was always true was not supported. SET, in contrast, makes no predictions about response rate, so it is not embarrassed by any particular result. Thus, in some of the cases noted, SET seems to ''win'' over both BeT and LeT, but as Whitaker et al. (2003) point out, it only does so by making no predictions at all about, for example, effects of motivational manipulations or relative response rates on mixed FI.

Being the most recent behavioral account of timing, ATM is necessarily the least well-tested. It is primarily a model of response timing, which makes predictions about DRL and FI performance, and as such, cannot account for stimulus timing in animals without further development, such as data collected with the frequently used bisection procedure (Church & Deluty, 1977). Some other limitations, discussed by Dragoi et al. (2003) themselves (e.g., p. 142) involve the inability to predict individual-trial data (e.g., Church et al., 1994). Like LeT, ATM also encounters problems with mixed-FI schedules, as independent timing of both the short and long components of mixed FI cannot be accounted for when the two components are very different (Dragoi et al., 2003). In practice, in this sort of situation (e.g., mixed FI 30 s FI 240 s), rats appear to have no difficulty producing response peaks at around the times of both components (Whitaker et al., 2003), thus apparently timing these two durations accurately. However, on the positive side, the ATM model may predict failures of superposition at long FI values (e.g., Dragoi et al.'s Figure 13) and, in fact, increases in coefficient of variation at long FI values are obtained in practice (Lejeune & Wearden, 1991), so this prediction actually may fit data better than the supposition of strict superposition at all FI values, which SET proposes.

As well as some empirical tests of behavioral models, discussed briefly above, another issue is how

*Published in Journal of the Experimental Analysis of Behavior (2006), vol. 85, n°1, pp. 125-142*
*DOI: 10.1901/jeab.2006.85.04*
*Status : Postprint (Author's version)*

behavioral the models really are. BeT uses an internal pacemaker to drive the transition between one adjunctive behavior and another, so the model depends on an internal process, although the pacemaker cannot be directly ''read'' by the organism, as in SET, so the pacemaker does not play a role in a cognitively based decision mechanism like the one SET uses. As mentioned above, attempts to identify the adjunctive behavior specified by BeT by direct observation have met with mixed success (see Fetterman et al., 1998 and Lejeune et al., 1998, for discussion), and questions about the behavioral nature of the states proposed by LeT also arise. LeT does not specify the mechanism by which the activation of successive states rises and falls, although a mathematical description of the change in state activation over time is provided, and the resulting functions bear a striking resemblance to those obtained from Grossberg and Schmajuk's (1989) ''spectral timing'' theory, which is a timing model based on hypothetical underlying neural processes. This raises the question of whether Machado's (1997) states are behavioral, or internal, even neural, entities. Can a theory be behavioral if the behavioral states on which it depends are internal events, which may have no other observable manifestation than the behavior they are postulated to explain?

The above brief review shows that the necessity for a cognitive structure like the clock, memory, and decision levels of SET for explanations of animal timing has been vigorously challenged over the last 20 years. However, the ability of recent behavioral models to fit timing data collected in many experiments has yet to be fully evaluated. One of the arguments put forward by proponents of such models is ''parsimony.'' Indeed, SET may seem, at first sight, a complicated multiprocess model, and as Staddon and Higa (1999) point out, not all parts of the ''erector set'' (p. 227) of SET are used in all cases; that is, different components of the model are called into play when necessary to account for the phenomenon at hand. More parsimonious models, however, may not be able to explain the complexity of timing behavior as obtained in contemporary experiments using operant methods.

Apparent failures of tests of what seem to be critical predictions of behavioral models, as well as difficulties in verifying them by direct observation (see Lejeune et al., 1998, for discussion) mean that behavioral theories like BeT, LeT, and ATM, in spite of their ingenious theoretical development and the fact that they sometimes provide striking instances of fit between data and theory, cannot be considered as having supplanted the leading cognitive model of animal timing, SET. A further difficulty with behavioral models is that adopting them would erode the proposition of animal/human continuity in the field of timing research that has proved to be so fruitful (Allan, 1998; Wearden, 2003). It is difficult to imagine humans performing on timing tasks that involve judgements of the duration of brief stimuli, sometimes presented only once (e.g., Wearden & Bray, 2001), by using chains of adjunctive activities, or the learning of associations, to generate their responses, although behavior on such tasks may be readily explained with reference to internal clock mechanisms.

## CONCLUDING COMMENTS

In this review, we have attempted to outline the methodological contributions of B. F. Skinner and those who later developed his methods to the study of animal timing. We presented a short review of various behavior-analytic accounts of animal timing data, which are considered by their authors consistent with Skinner's general theoretical position about the control of behavior, although the models do not derive directly from any theoretical treatment of temporal control given by Skinner in either *The Behavior of Organisms* or *Schedules of Reinforcement.* The debt that the field of animal timing owes to Skinner is immense, although in his writings he seemed consistently more interested in the response rates generated by schedules with temporal periodicities and constraints than by issues of temporal control, still less the conformity of animal performance to psychophysical laws like the power law and Weber's Law. Research since the 1970s has been dominated largely by those issues, but a reexamination of Skinner's work, particularly in *The Behavior of Organisms* but also *Schedules of Reinforcement*, may make a contemporary reader wonder why some lines of research have been pursued so assiduously, whereas others (particularly the study of response rate on schedules like FI) have been neglected. Modern theories of temporal control in animals, like SET and its competitors, have produced instances in which the correspondence between the predictions of theoretical models and data is almost supernaturally good, but perhaps this almost miraculous goodness of fit has been obtained at the price of neglecting some potentially important phenomena, and it may be that the work of Skinner on timing in animals still has something to teach us today.

## REFERENCES

Allan, L. (1998). The influence of the scalar timing model on human timing research. *Behavioural Processes, 44,* 101-117.

Anger, D. (1963). The role of temporal discrimination in the reinforcement of Sidman avoidance behavior. *Journal of the Experimental Analysis of Behavior, 6,* 477-506.

Baum, W. M. (1973). The correlation-based law of effect. *Journal of the Experimental Analysis of Behavior, 20,* 137-153.

Beam, J. B., Killeen, P. R., Bizo, L. A., & Fetterman, G. J. (1998). How reinforcement context affect temporal production and categorization. *Animal Learning and Behavior*, *26*, 388-398.

Bizo, L. A., & White, K. G. (1994a). The behavioral theory of timing: Reinforcer rate determines pacemaker rate. *Journal of the Experimental Analysis of Behavior, 61,* 19-34.

Bizo, L. A., & White, K. G. (1994b). Pacemaker rate in the behavioral theory of timing. *Journal of Experimental Psychology: Animal Behavior Processes, 20,* 308-321.

Bizo, L. A., & White, K. G. (1995). Biasing the pacemaker in the behavioural theory of timing. *Journal of the Experimental Analysis of Behavior*, *64*, 225-236.

Bizo, L. A., & White, K. G. (1997). Timing with controlled reinforcer density: Implications for models of timing. *Journal of Experimental Psychology: Animal Behavior Processes, 23,* 44-55.

Blomeley, F. J., Lowe, C. F., & Wearden, J. H. (2004). Reinforcer concentration effects on a fixed-interval schedule. *Behavioural Processes, 67,* 55-66.

Brown, B. L., Hemmes, N. S., Cabeza de Vaca, S. C., & Pagano, C. (1993). Sign and goal tracking during delay and trace autoshaping in pigeons. *Animal Learning and Behavior*, *21*, 360-368.

Brown, P. L., & Jenkins, H. M. (1968). Auto-shaping of the pigeon's keypeck. *Journal of the Experimental*

*Analysis of Behavior*, *11*, 1-8.

Buhusi, C., & Meck, W. H. (2000). Timing for the absence of the stimulus: The gap paradigm revisited. *Journal of Experimental Psychology: Animal Behavior Processes*, *26*, 305-322.

Catania, A. C. (1970). Reinforcement schedules and psychophysical judgments: A study of some temporal properties of behavior. In W. N. Schoenfeld (Ed.), *The theory of reinforcement schedules* (pp. 1-42). New York: Appleton-Century-Crofts.

Church, R. M. (1984). Properties of the internal clock. In L. Allan, &J. Gibbon (Eds.), *Timing and time perception* (pp. 566-582). New York: Annals of the New York Academy of Sciences.

Church, R. M., & Deluty, M. Z. (1977). Bisection of temporal intervals. *Journal of Experimental Psychology: Animal Behavior Processes*, *3*, 216-228.

Church, R. M., Meck, W. H., & Gibbon, J. (1994). Application of scalar timing theory to individual trials. *Journal of Experimental Psychology: Animal Behavior Processes*, *20*, 135-155.

Dews, P. B. (1962). The effects of multiple SD periods on responding on a fixed-interval schedule. *Journal of the Experimental Analysis of Behavior, 5,* 369-374.

Dews, P. B. (1965). The effect of multiple SD periods on responding on a fixed-interval schedule: III. Effects of changes in patterns of interruption, parameters and stimuli. *Journal of the Experimental Analysis of Behavior, 8,* 427-433.

Dews, P. B. (1970). The theory of fixed-interval responding. In W. N. Schoenfeld (Ed.), *The theory of reinforcement schedules* (pp. 43-61). New York: AppletonCentury-Crofts.

Dragoi, V., Staddon, J. E. R., Palmer, R. G., & Buhusi, C. V. (2003). Interval timing as an emergent learning property. *Psychological Review, 110,* 126-144.

Drew, M. R., Zupan, B., Cooke, A., Couvillon, P. A., & Balsam, P. D. (2005). Temporal control in conditioned responding in goldfish. *Journal of Experimental Psychology: Animal Behavior Processes, 31,* 31-39.

Eisler, H. (1976). Experiments on subjective duration 1868-1975: A collection of power function exponents. *Psychological Bulletin, 83,* 1154-1171.

Falk, J. L. (1977). The origin and functions of adjunctive behavior. *Animal Learning and Behavior, 5,* 325-335.

Ferster, C. B., & Skinner, B. F. (1957). *Schedules of reinforcement.* New York: Appleton-Century-Crofts.

Fetterman, J. G., & Killeen, P. (1991). Adjusting the pacemaker. *Learning and Motivation, 22,* 226-252.

Fetterman, J. G., & Killeen, P. (1995). Categorical scaling of time: Implications for clock counter models. *Journal of Experimental Psychology: Animal Behavior Processes*, *21*, 43-63.

Fetterman, J. G., Killeen, P. R., & Hall, S. (1998). Watching the clock. *Behavioural Processes, 44,* 211-224.

Frank, J., & Staddon, J. E. R. (1974). Effects of restraint on temporal discrimination behavior. *The Psychological Record*, *24*, 123-130.

Gallistel, R., & Gibbon, J. (2000). Time, rate, and conditioning. *Psychological Review, 107,* 289-344.

Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological Review*, *84*, 279-325.

Gibbon, J. (1991). Origins of scalar timing. *Learning and Motivation*, *22*, 3-38.

Gibbon, J., & Allan, L. (1984). *Timing and time perception*. New York: Annals of the New York Academy of Sciences.

Gibbon, J., & Balsam, P. (1981). Spreading association in time. In C. M. Locurto, H. S. Terrace, & J. Gibbon (Eds.), *Autoshaping and conditioning theory* (pp. 219254). New York: Academic Press.

Gibbon, J., Church, R. M., & Meck, W. H. (1984). Scalar timing in memory. In L. Allan, & J. Gibbon (Eds.), *Timing and time perception* (pp. 52-77). New York: Annals of the New York Academy of Sciences.

Gibbon, J., & Fairhurst, S. (1994). Ratio versus difference comparators in choice. *Journal of the Experimental Analysis of Behavior, 62,* 409-434.

Gibson, J. J. (1975). Events are perceivable but time is not. In J. T. Fraser, & N. Lawrence (Eds.), *The study of time II. Proceedings of the Second Conference of the International Society for the Study of Time* (pp. 295-301). Berlin, Germany: Springer-Verlag.

Glazer, H., & Singh, D. (1971). Role of collateral behavior in temporal discrimination performance and learning. *Journal of Experimental Psychology, 91,* 78-84.

Grossberg, S., & Schmajuk, N. A. (1989). Neural dynamics of adaptive timing and temporal discrimination during associative learning. *Neural Networks*, *2*, 79-102.

Hearst, E., & Jenkins, H. M. (1974). *Sign-tracking: The stimulus-reinforcer relation and directed action.* Austin, TX: Psychonomic Society.

Jasselette, P., Lejeune, H., & Wearden, J. H. (1990). The perching response and the laws of animal timing. *Journal of Experimental Psychology: Animal Behavior Processes*, *16*, 150-161.

Killeen, P., Bizo, L. A., & Hall, S. (1999). A clock not wound runs down. *Behavioural Processes*, *45*, 129-139.

Killeen, P., & Fetterman, J. G. (1988). A behavioral theory of timing. *Psychological Review*, *95*, 274-295.

Killeen, P., & Fetterman, J. G. (1993). The behavioral theory of timing: Transition analyses. *Journal of the Experimental Analysis of Behavior*, *59*, 411-422.

Kirkpatrick, K. (2002). Packet theory of conditioning and timing. *Behavioural Processes, 57,* 89-106.

Kirkpatrick, K., & Church, R. M. (2000). Independent effects of stimulus and cycle duration in conditioning: The role of timing processes. *Animal Learning and Behavior*, *28*, 373-388.

Kirkpatrick, K., & Church, R. M. (2004). Temporal learning in random control procedures. *Journal of Experimental Psychology: Animal Behavior Processes*, *30*, 213-228.

Kuch, D. O. (1974). Differentiation of press duration with upper and lower limits for reinforced values. *Journal of the Experimental Analysis of Behavior*, *22*, 275-283.

Laties, V. G., Weiss, B., & Weiss, A. B. (1969). Further observation of ‘‘overt’’ mediating behavior and the discrimination of time. *Journal of the Experimental Analysis of Behavior*, *12*, 43-57.

Leak, T., & Gibbon, J. (1995). Simultaneous timing of multiple intervals: Implications of the scalar property. *Journal of Experimental Psychology: Animal Behavior Processes*, *21*, 3-19.

Lejeune, H. (1990). Timing: Differences in continuity or generality beyond differences? In D. Blackman, & H. Lejeune (Eds.), *Behaviour analysis in theory and practice: Contributions and controversies* (pp. 53-90). London: Erlbaum.

Lejeune, H., Cornet, S., Ferreira, M. A., & Wearden, J. H. (1998). How do mongolian gerbils (*Meriones* *unguiculatus*) pass the time? Adjunctive behavior during temporal differentiation in gerbils. *Journal of Experimental Psychology: Animal Behavior Processes*, *24*, 352-268.

Lejeune, H., Ferrara, A., Simons, F., & Wearden, J. H. (1997). Adjusting to changes in the time of reinforcement: Peak-interval transitions in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, *23*, 211-231.

Lejeune, H., Huynen, M-C., & Ferrara, A. (2000). Temporal differentiation in two strains of small rodents: A wood mouse (*Apodemus sylvaticus*) and an albino mouse (*Mus musculus* OF1). *Behavioural Processes*, *52*, 155-169.

Lejeune, H., & Richelle, M. (1982). Differential reinforcement of perching duration in the pigeon: A comparison with differential-reinforcement-of-low-rate keypecking. *Behaviour Analysis Letters*, *2*, 49-57.

Lejeune, H., & Wearden, J. H. (1991). The comparative psychology of fixed-interval performance: Some quantitative analyses. *Learning and Motivation*, *22*, 84-111.

Lejeune, H., & Wearden, J. H. (2005). *Scalar properties in animal timing: Conformities and violations*. Manuscript submitted for publication.

Lowe, C. F., & Harzem, P. (1977). Species differences in temporal control of behavior. *Journal of the Experimental Analysis of Behavior*, *28*, 189-201.

Machado, A. (1997). Learning the temporal dynamics of behavior. *Psychological Review*, *104*, 241-265.

Machado, A., & Cevik, M. (1998). Acquisition and extinction under periodic reinforcement. *Behavioural Processes*, *44*, 237-262.

Nevin, J. A., & Berryman, R. (1963). A note on chaining and temporal discrimination. *Journal of the Experimental Analysis of Behavior, 6,* 109—113.

Pavlov, I. P. (1927). *Conditioned reflexes.* (G. V. Anrep, Trans.). London: Oxford University Press.

Platt, J. R. (1979). Temporal differentiation and the psychophysics of time. In M. D. Zeiler, & P. Harzem (Eds.), *Advances in the analysis of behaviour, Vol. 1: Reinforcement and the organization of behaviour* (pp. 129). Chichester, England: Wiley.

Platt, J. R., & Scott, G. K. (1981). Analysis of the superiority of discrete-trials over free-operant procedures in temporal differentiation. *Journal of Experimental Psychology: Animal Behavior Processes,* 7, 269—277.

Richelle, M. (1968). Notions modernes de rythmes biologiques et regulations temporelles acquises. In J. de Ajuriaguerra (Ed.), *Cycles biologiques et psychiatrie* (pp. 233-255). Geneve: Georg et Cie. Paris: Masson.

Richelle, M., & Lejeune, H. (Eds.). (1980). *Time in animal behaviour* London: Pergamon Press.

Richelle, M., & Lejeune, H. (1984). Timing competence and timing performance: A comparative approach. In J. Gibbon, & L. Allan (Eds.), *Timing and time perception* (pp. 254-268). New York: Annals of the New York Academy of Sciences.

Richelle, M., Lejeune, H., Perikel, J. J., & Fery, P. (1985). From biotemporality to nootemporality: Towards an integrative and comparative view of time in behavior. In J. A. Michon, &J. L. Jackson (Eds.), *Time, mind and behavior* (pp. 75-99). Berlin/Heidelberg: Springer.

Roberts, S. (1981). Isolation of an internal clock. *Journal of Experimental Psychology: Animal Behavior Processes*, *7*, 242-268.

Roper, T. J. (1981). What is meant by the term ''schedule- induced'' and how general is schedule induction? *Animal Learning and Behavior, 9,* 433-440.

Savastano, H. I., & Miller, R. R. (1998). Time as content in Pavlovian conditioning. *Behavioural Processes, 44,* 147-162.

Schoenfeld, W. N. (Ed.). (1970). *The theory of reinforcement schedules* New York: Appleton-Century-Crofts.

Schwartz, B., & Gamzu, E. (1977). Pavlovian control of operant behavior. In W. K. Honig, & J. E. R. Staddon (Eds.), *Handbook of operant behavior* (pp. 53-97). Englewood Cliffs, NJ: Prentice Hall.

Segal-Rechtschaffen, E. (1963). Reinforcement of mediating behavior on a spaced-responding schedule. *Journal of the Experimental Analysis of Behavior*, *6*, 39-46.

Skinner, B. F. (1938). *The behavior of organisms: An experimental analysis*. New York: Appleton-Century-Crofts.

Skinner, B. F. (1948). ''Superstition'' in the pigeon. *Journal of Experimental Psychology, 38,* 168-172.

Skinner, B. F. (1956). A case history in scientific method. *American Psychologist*, *11*, 221-233.

Staddon, J. E. R. (1965). Some properties of spaced responding in pigeons. *Journal of the Experimental Analysis of Behavior*, *8*, 19-27.

Staddon, J. E. R. (1977). Schedule-induced behavior. In W.

K. Honig, & J. E. R. Staddon (Eds.), *Handbook of operant behavior* (pp. 125-153). Englewood Cliffs, NJ: Prentice-Hall.

Staddon, J. E. R., Chelaru, I. M., & Higa, J. J. (2002). A tuned-trace theory of interval-timing dynamics. *Journal of the Experimental Analysis of Behavior*, *77*, 105-124.

Staddon, J. E. R., & Higa, J. J. (1999). Time and memory: Towards a pacemaker-free theory of interval timing. *Journal of the Experimental Analysis of Behavior*, *71*, 215-252.

Staddon, J. E. R., & Simmelhag, V. L. (1971). The ''superstition'' experiment: A re-examination of its implications for the principles of adaptive behavior. *Psychological Review*, *78*, 3-43.

Stubbs, A. (1979). Temporal discrimination and psychophysics. In M. D. Zeiler, & P. Harzem (Eds.), *Advances in the analysis of behaviour, Vol. 1: Reinforcement and the organization of behaviour* (pp. 341-369). Chichester, England: Wiley.

Wearden, J. H. (1991). Do humans possess an internal clock with scalar timing properties? *Learning and Motivation, 22,* 59-83.

Wearden, J. H. (1999). ''Beyond the fields we know...'': Exploring and developing scalar timing theory. *Behavioural Processes, 45,* 3-21.

Wearden, J. H. (2003). Applying the scalar timing model to human time psychology: Progress and challenges. In H. Helfrich (Ed.), *Time and mind II: Informationprocessing perspectives* (pp. 21-39). Seattle, WA: Hogrefe & Huber.

Wearden, J. H. (2004). Decision processes in models of timing. *Acta Neurobiologiae Experimentalis*, *64*, 303-317.

Wearden, J. H., & Bray, S. (2001). Scalar timing without reference memory: Episodic temporal generalization and bisection in humans. *Quarterly Journal of Experimental Psychology*, *54B*, 289-310.

*Published in Journal of the Experimental Analysis of Behavior (2006), vol. 85, n°1, pp. 125-142*
*DOI: 10.1901/jeab.2006.85.04*
*Status : Postprint (Author's version)*

Wearden, J. H., & Clark, R. B. (1988). Interresponse-time reinforcement and behavior under periodic reinforcement schedules: A case study using computer modeling. *Journal of Experimental Psychology: Animal Behavior Processes*, *14*, 200-211.

Wearden, J. H., & McShane, B. (1988). Interval production as an analogue of the peak procedure: Evidence for similarity of human and animal timing processes. *Quarterly Journal of Experimental Psychology, 40B,* 363-375.

Whitaker, J. S., Lowe, C. F., & Wearden, J. H. (2003). Multiple-interval timing in rats: Performance on two-valued mixed fixed-interval schedules. *Journal of Experimental Psychology: Animal Behavior Processes*, *29*, 277-291.

Wilson, M. P., & Keller, F. S. (1953). On the selective reinforcement of spaced responding. *Journal of Comparative and Physiological Psychology*, *46*, 190-193.

Wynne, C. D. L., & Staddon, J. E. R. (1988). Typical delay determines waiting time on a periodic-food schedule: Static and dynamic tests. *Journal of the Experimental Analysis of Behavior*, *50*, 197-210.

Wynne, C. D. L., Staddon, J. E. R., & Delius, J. D. (1996). Dynamics of waiting in the pigeon. *Journal of the Experimental Analysis of Behavior*, *65*, 603-618.

Zeiler, M. D. (1985). Pure timing in temporal differentiation. *Journal of the Experimental Analysis of Behavior*, *43*, 183-193.

Zeiler, M. D., & Harzem, P. (1979). *Advances in analysis of behaviour, Vol. 1: Reinforcement and the organization of behaviour*. Chichester, England: Wiley.

Zuriff, G. E. (1969). Collateral responding during differential reinforcement of low rates. *Journal of the Experimental Analysis of Behavior*, *12*, 971-976.