A tribute to John Gibbon

Russell M. Church *

Department of Psychology, Box 1853, Brown University, Providence, RI 02912, USA

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Abstract

This article provides an overview of the published research of John Gibbon. It describes his experimental research on scalar timing and his development of scalar timing theory. It also describes his methods of research which included mathematical analysis, conditioning methods, psychophysical methods and secondary data analysis. Finally, it describes his application of scalar timing theory to avoidance and punishment, autoshaping, temporal perception and timed behavior, foraging, circadian rhythms, human timing, and the effect of drugs on timed perception and timed performance of Parkinson’s patients. The research of Gibbon has shown the essential role of timing in perception, classical conditioning, instrumental learning, behavior in natural environments and in neuropsychology. © 2002 Published by Elsevier Science B.V.

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1. Introduction

There was a remarkable breadth to John Gibbon’s research, but also a single focus. The topics of his research included avoidance, punishment, autoshaping, temporal perception and timed behavior, foraging, circadian rhythms, and Parkinson’s disease. He studied the behavior of pigeons, rats, ring doves, starlings and adult and infant human participants. He used the methods of psychophysics, animal learning, mathematical psychology, secondary data analysis and neuropsychology and he published experimental reports, mathematical analyses, review articles, and theoretical articles. Despite this breadth of topic, species, method and approach, the focus of nearly all of his research was on timing, particularly scalar timing theory (Fig. 1).

2. Scalar timing theory

In an article entitled ‘Origins of scalar timing’, Gibbon (1991) provided both an historical description and a causal introduction to scalar tim-
Fig. 1. John Gibbon (12 February, 1934–16 January, 2001).

Scalar timing is proposed as the basic latency mechanism underlying asymptotic free-operant avoidance performance (p. 109). The assumptions were that avoidance responses are estimates of the time of the next shock, and time estimates are scale transforms of a single stochastic process. This was described as a Weber-like assumption about timing that may be tested. The mathematical sections of this article were based on a model of free-operant avoidance performance as a semi-Markov chain. The tests of the predictions of this model were based on secondary data analysis. For example, the simplest prediction from the scalar assumption is that the mean of a behavioral estimate of time will increase proportionally with the interval to be timed. From the published literature, Gibbon found that the latency of the avoidance response was approximately linearly related to the interval between stimulus and shock (Fig. 2). He noted that a more stringent test of the scalar assumption would be the superposition of the form of the avoidance latency distributions for different stimulus-shock training conditions, if time were scaled in proportional units. This was also supported by secondary data analysis. These ideas, with some extensions, were made more accessible to psychologists in an article in the Psychological Review (Gibbon, 1972).

Fig. 2. Proportional timing. The latency of avoidance responding was a function of the duration of warning signal in three avoidance experiments. From Gibbon (1971).
In his next article in the *Psychological Review* (Gibbon, 1977), he greatly expanded the application of scalar timing. Previously it had been focused on avoidance latencies, but in this article scalar timing was also applied to fixed-interval schedules of positive reinforcement, fixed-time schedules of reinforcement, concurrent schedules of reinforcement, discrimination between stimulus durations, and choice between delays of reinforcement. Secondary data analysis was used to support four consequences of scalar timing:

(a) Proportional timing. The mean of an estimate of a duration increased linearly with the duration to be estimated,
(b) Scalar standard deviation. The standard deviation of an estimate of a duration increased linearly with the duration to be estimated,
(c) Constant coefficient of variation. The coefficient of variation of an estimate of a duration (the standard deviation divided by the mean) was a constant, irrespective of the duration to be estimated, and
(d) Superposition. The distributions of an estimate of a duration based on different durations to be estimated will be the same if relative time is used (duration divided by duration to be estimated).

In addition to its extension of the scalar property to a wide range of experimental procedures, 'Weber’s law in animal timing,’ this article introduced ‘Scalar expectancy theory.’ The former was a cognitive process; the latter was a motivational one. The motivational process was quantified by an expectancy ratio of local and global expected time to reinforcement. The concept of threshold of the expectancy ratio was also introduced, such that timing behavior was assumed to begin after this threshold was crossed.

### 2.2. Information processing model of scalar timing theory

An information-processing version of scalar timing theory was used in an experiment in a temporal choice procedure (Gibbon and Church, 1981) and a temporal generalization procedure (Church and Gibbon, 1982). Both of these articles were characterized by data from timing experiments with quantitative variations in independent variables, appendices containing the derivation of predictions, and comparisons of observations with predictions. Two chapters described the theory in more detail, and described the effects of different sources of variation (Gibbon and Church, 1984; Gibbon et al., 1984b) (Fig. 3). In the information-processing version of scalar timing theory there are three major parts: clock, memory, and decision. The clock consists of a pacemaker, a switch, and an accumulator. When a stimulus occurs the pulses from the pacemaker may enter the accumulator (depending on the state of the switch); thus, the number of pulses in the accumulator represent the perceived time. For memory storage, at reinforcement, the number of pulses in the accumulator (perhaps multiplied by a variable) is transferred to the reference memory. For memory retrieval, a random sample of a single stored element is compared to the number of pulses in the accumulator. For a decision, a ratio of the absolute value of the difference between the sample from memory and the perceived current time, and the sample from memory is obtained. This is compared with a sample from a distribution of thresholds (normally distributed with some mean and standard deviation), and a response occurs if the ratio is less than the threshold.

The purposes of these two chapters were to describe the information-processing model of scalar timing, and to determine which sources of variance (clock, memory, and decision), which types of variance (Poisson, scalar), and which decision rule (absolute and relative) were consistent with the data. Approximately scalar timing performance could occur with many sources being nonscalar; this received the most thorough analysis by Gibbon (1992).

To account for the quantitative results of some experimental procedures, modifications of the original proposals were proposed. Some research with variable intervals suggested that different decision rules may be necessary for different reinforcement schedules (Brunner et al., 1997). Research on the reinforcement omission effect suggested that food resets the clock more completely than the presentation of a stimulus associated with food (Mellon et al., 1995).
One of the essential ideas of scalar timing theory was that performance was controlled by a threshold (Gibbon, 1977; Gibbon et al., 1984b; Gibbon, 1991). In the fixed-interval procedure this means that an individual trial would be characterized by a period of a relatively constant low rate of responding followed by a period of a relatively constant high rate of responding as described by Schneider (1969). This leads to a step function between the time of transition between the low and high rates of response on individual trials. Because the time of transition between the low and high rate of responding was variable, the mean response rate would have a gradual increase. This same analysis was applied to the temporal generalization procedure and the peak procedure (Fig. 4).

In research in the 1980’s Gibbon and his colleagues assumed that performance on an individual trial of the peak procedure would be characterized by a low response period, followed by a high response period that normally included the time at which food would be delivered, which was followed by another low response period. This was subsequently examined empirically (Gibbon and Church, 1990; Gibbon and Church, 1992; Church et al., 1994). These data were supportive of the hypothesis that the animal went through three response-rate states (low, high, and low) on each nonreinforced trial of a peak procedure. This state analysis made it possible to identify two transition times—the time of the start of the high response rate (start), the time of the end of the high response rate (stop), the mean time between the start and end (middle) and the time from the start to the end (spread). In these articles, the correlation pattern among the starts, stops, middles, and spreads were used to quantitatively assess the contributions of memory and threshold sources of variance. This analysis was extended to reinforcement of multiple intervals (Leak and Gibbon, 1995).
3. Methods

Gibbon used a unique combination of the approaches of mathematical psychology, animal conditioning, psychophysics, and secondary analysis to reach conclusions about behavior.

3.1. Mathematical analysis

His first article, with William McGill, was an analysis of a multistage process consisting of exponentially distributed components, each with a unique decay constant (McGill and Gibbon, 1965). An important feature of this article was that the authors obtained an explicit solution that required a clear understanding of the problem, and some calculus and probability theory. This general gamma distribution was applied to simple reaction time results. It was subsequently used in the analysis of the interlick interval of rats and the intertap interval of human participants attempting to tap at a regular interval (Church et al., 1992).

Gibbon published three additional articles in the Journal of Mathematical Psychology (Gibbon, 1971, 1981a, 1992). The method in each of them was to describe a problem and a precise description of a process, to obtain an explicit solution of the problem, and to compare the output of the model with the behavior of animals.

Whenever possible, he tried to obtain explicit solutions rather than rely upon simulations of a process. The solutions were often presented as short appendices to articles, with the equations expressing the conclusions integrated into the body of the text. He preferred explicit solutions because they provided exact answers to well-specified problems, and the resulting equations could be used for a rapid comparison of the data with a model at many different values of the parameters. He also found that the problems presented interesting intellectual challenges, and that the solutions were often aesthetically pleasing.

3.2. Experimental methods

Gibbon was eclectic in his choice of experimental methods. His empirical research began with the operant psychology methods that included informal within-subject experimental designs, individual subject analyses, experimental control rather than statistical evaluation, etc. But in research on autoshaping, and in subsequent research, he used more formal experimental designs, group comparisons, and statistical evaluation. Some of his research used psychophysical methods in which the value of a dependent variable was functionally related to the value of an independent variable. Presumably a good theory should account for replicable results obtained from any of these methods. Regardless of the experimental method, he focused his efforts on the theoretical explanation of the asymptotic results.

3.3. Secondary data analysis

Although it is standard practice for psychologists to read articles related to their research, many consider it sufficient to understand the method, a summary of the results, and an au-
4. Topics

4.1. Avoidance and punishment

His PhD thesis was an experimental study of avoidable and unavoidable shock (Gibbon, 1967). It described conditions under which ‘punishment was less effective in suppressing behavior when shock was inevitable on every trial than when waiting in the warning stimulus avoided shock’ (p. 458). On avoidance and punishment, he also published four additional experimental studies (Fairhurst and Gibbon, 1983; Flye and Gibbon, 1979; Gibbon and Hunt, 1972; Neffinger and Gibbon, 1975), a theoretical article (Gibbon, 1972), and a chapter (Gibbon, 1979). The theoretical article and the chapter contained many of the basic ideas of scalar timing, and they contained many of the features of his later articles. These included a statement of the assumptions of the theory, diagrams of the theory, equations, figures that compared the predictions of the theory with published experimental results, and a mathematical appendix to prove that the equations followed from the assumptions. In this theoretical article and chapter Gibbon did not cite any of his own experiments on avoidance and punishment. The basic ideas of scalar timing were apparently developed by Gibbon on the basis of his analysis of the published data of many investigators of avoidance and punishment.

In addition to scalar expectancy theory, he analyzed the concept of contingency in both classical and instrumental conditioning (Gibbon et al., 1974). This provided a geometric representation of classical and instrumental conditioning procedures, and an evaluation of statistical indices of the contingencies between stimuli, responses, and reinforcers. This analysis was used in the design and analysis of two of the experiments on avoidance (Flye and Gibbon, 1979; Neffinger and Gibbon, 1975) and in subsequent experiments on autoshaping and other conditioning procedures.

4.2. Autoshaping

Beginning in 1975, Gibbon published a series of experimental studies of autoshaping in pigeons in collaboration with Peter Balsam, Charles Locurto, Herbert Terrace and others. The autoshaping procedure is a classical conditioning procedure in which food delivery (the US) is contingent upon a lighted key (the CS), but not upon keypeck responses (the CR). Gibbon and his colleagues studied the effect of variables, many of them temporal variables, on the speed of acquisition of the autoshaped response, and the mean and the gradient of the response rate during the stimulus.

The first empirical studies in this series demonstrated that the speed of acquisition and the re-
response strength (as measured by the probability of a response during the stimulus, and the rate of responding during the stimulus) of the pigeon’s autoshaped response increased as the interval between successive reinforcements increased (Gibbon et al., 1975; Terrace et al., 1975). In an influential study that combined new experiments with 200 pigeons and extensive secondary data analysis (see Fig. 5), it was found that the number of reinforcements necessary for pigeons to reach a criterion of acquisition of autoshaping was a function of the ratio of two time intervals, rather than either one alone (Gibbon et al., 1977). Acquisition was facilitated by short-duration stimuli, and long durations between reinforcements; it was better predicted by the ratio of the latter to the former than by either of them alone. In an understated sentence, the authors wrote, ‘The ratio effect may require some fundamental rethinking about the associative learning process in autoshaping’ (p. 281). This fundamental rethinking culminated in a review article entitled, ‘Time, rate and conditioning’ (Gallistel and Gibbon, 2000).

There were several studies in which responses persisted during the stimulus although they prevented the delivery of food at the end of the interval (Locurto et al., 1976, 1978). Other conditioning manipulations included delay of reinforcement (Locurto et al., 1980a), partial reinforcement (Gibbon et al., 1980), restriction of movement (Locurto et al., 1980b), preexposure to the reinforcer with or without random presentations of the stimulus (Balsam et al., 1980), and trace conditioning (Balsam and Gibbon, 1982). The studies also included interference effects (Balsam and Gibbon, 1988; Straub and Gibbon, 1983), and ways to reduce interference (Cooper et al., 1990). The most recent study showed that, in extinction, overall responsiveness was greatly diminished but the temporal gradients remained (Ohyama et al., 1999).

Gibbon and Balsam (1981) developed a theory of the conditioning process that involves an analysis of the temporal intervals of the stimulus and the reinforcement, and the overall expectancy of a reinforcement. The first sentence of this chapter was ‘Learning and timing are related intimately’ p. 219. The treatment of the temporal intervals involved in autoshaping provided a way to understand the effects of the contingency between stimulus and reinforcement (Gibbon, 1981b). Much of the research is summarized, integrated, and explained in Locurto et al. (1981).

The ideas that were originally developed to account for autoshaping, along with further developments in an information-processing version of scalar timing theory and Gallistel’s rate expectancy theory, were extended to account for the results of a wide range of conditioning procedures (Gallistel and Gibbon, 2000). These include classical conditioning (acquisition, extinction, and asymptotic behavior of single and multiple stimuli), operant choice, and many other phenomena. The conceptual framework described in this article provides a computational approach to the explanation of a wide range of phenomena that is fundamentally different from the principles of association that are typically used. (See Gallistel and Gibbon, 2001, for a brief description of distinctions between computational and associative models.)

4.3. Temporal perception and timed behavior

Prior to 1981 Gibbon’s empirical research was focused on two problems: the determinants of aversive behavior and autoshaping. In both cases he found that the explanation of the behavior required an understanding of animal timing. Initially he applied the principles of scalar timing to aversive behavior and autoshaping, but he clearly recognized that these were only examples of the pervasive influence of scalar timing on the behavior of animals (Gibbon, 1977). Beginning in 1981 he turned his attention directly to the study of time perception and timed performance. He asked such questions as, ‘What is the functional relationship between physical time and subjective time?’ ‘What is the relationship between temporal perception and temporal memory?’ and ‘What is the basis for a decision about the duration of a stimulus, or whether it was time to make a response?’ This was a focus on questions about temporal perception, temporal memory, and temporal decision. Most of the experimental evidence came from three types of timing procedures: tem-
poral differentiation, time discrimination, and choice procedures.

In a temporal differentiation procedure, there is differential reinforcement of responses that occur at a particular time. For example, in the peak procedure, the first response that occurs after a fixed time after stimulus onset is reinforced with some probability, and others are never reinforced. The response gradients usually increase to a maximum near the time of reinforcement and then decrease with a small asymmetry (Church et al., 1991). The basic results and the interpretation of the results based on scalar timing theory were described in the section on scalar timing theory.

In a time discrimination procedure, a stimulus is presented for some duration and a particular response is reinforced. For example, in the temporal generalization procedure (Church and Gibbon, 1982), reinforcement may follow a response that occurs after a 4-s white noise stimulus, but not after stimuli that are longer or shorter than 4 s. Most time discrimination experiments have used the bisection procedure in which one response is reinforced following a short-duration stimulus (e.g. 2 s), another response is reinforced following a long-duration stimulus (e.g. 8 s), and neither response is reinforced following stimuli of intermediate durations. The results are often plotted as a psychophysical function relating the probability of a particular response to the stimulus duration. The psychophysical function has the form of an ogive that is approximately symmetrical on a logarithmic scale, with a point of bisection near the geometric mean of the two extreme intervals. The mean and standard deviation of the point of bisection are approximately linear functions of the geometric mean of the extreme stimuli so that the ratio of the standard deviation to the mean is relatively constant. The general principle is that, if time is scaled relative to the geometric mean, the psychophysical functions approximately superimpose. Thus the same principles of proportional timing, scalar standard deviation, constant coefficient of variation, and superposition that were described for the temporal peak procedure also are present in the temporal bisection procedure. These principles also apply to number discrimination, and the same mechanisms may be responsible for time and number discrimination (Meck et al., 1985).

The major empirical difference between the temporal peak and temporal bisection functions were that the former were approximately symmetrical on a linear scale of time and the latter were approximately symmetrical on a logarithmic scale. In an analysis of several specific assumptions regarding the relationship of subjective to physical time, and regarding the decision rule for responding, Gibbon (1981a,c) found that only some combinations were consistent with the data.

In a choice procedure, an animal may make either of two responses that have different temporal consequences. Although most theoretical accounts of choice are based on molar principles such as the matching of the rate of the two responses with the rate of reinforcement of the two responses, a process explanation of the results in terms of scalar timing theory is plausible (Gallistel and Gibbon, 2000; Gibbon et al., 1988; Rachlin et al., 1986). A similar approach was used for the analysis of choice between variable and fixed delays with different reward amounts (Brunner et al., 1994), and in a potential resolution of a counterintuitive finding regarding the dynamics of time matching (Gibbon, 1995).

Gibbon considered the quantitative psychophysical relationship between subjective and physical time to be a fundamental problem of the psychology of timing, but a difficult one to resolve. A problem was that one could assume any transformation, if an inverse transformation were available. A possible solution was the ‘time-left’ procedure that may require the animal to take a difference between two subjective intervals, and compare the difference to a standard interval. The conclusion from this experiment was that subjective time was linear in physical time, with a scalar memory variance (Gibbon and Church, 1981). An overview of the nature of subjective time is provided by Gibbon (1986). Although it is possible that the scalar property is introduced at the level of the clock, even with a Poisson clock there are many ways in which the scalar property can emerge (Gibbon, 1992). An important one is a ratio (rather than a difference) decision rule. This was found to be important in multiple schedules.
of reinforcement (Aronson et al., 1993). In an explicit comparison of ratio and difference comparison rules in combination with three dependent variables (delay to food, the reciprocal of the delay to food, and the rate of food), Gibbon and Fairhurst, 1994 found that the quantitative preference functions in the time-left procedure were compatible with ratio comparisons, but not with difference comparisons.

4.4. Foraging

One of the concerns about the study of animal timing is that it may have no functional value in naturalistic environments. In collaboration with Alex Kacelnik, Doni Brunner and others, Gibbon demonstrated the close relationship between timing and the problems confronting an animal foraging for food. One possibility was that, through evolution, the animal became capable of learning to be an optimal forager; an alternative is that the animal had constraints on its perceptual, memory, and decision processes.

The foraging experiments were typically conducted with wild-caught starlings in room-sized environments. The description of the task and the behavior used terms such as ‘giving up time,’ ‘patch departure,’ and the articles were usually published in Animal Behaviour (Brunner and Gibbon, 1995; Brunner et al., 1992, 1996; Shettleworth et al., 1988). The same scalar timing theory was used to describe the foraging behavior of starlings in semi-naturalistic situations that was used to describe temporal discriminations of pigeons in operant conditioning boxes (Kacelnik et al., 1990).

4.5. Circadian rhythms

Gibbon maintained an interest in the relationship between interval and circadian timing systems. He thought of them as separate timing mechanisms with different characteristics. An interval timer was an accumulation process that had the scalar property and could be reset at any arbitrary time; in contrast, the circadian timer was a self-sustaining oscillation that was extremely accurate within a narrow range of entrainment. Both of them provided a basis for anticipatory behavior, and interactions between the two types of clocks could be observed (Gibbon et al., 1984a; Terman et al., 1984). The most recent statement of his views of the relationship between the interval and circadian timing systems is in a chapter (Gibbon et al., 1997a). This chapter also contains some new experimental data that suggests that, normally, an averaging of information from two independent sources would increase accuracy, but experimental conditions can be arranged such that the animal anticipates food at a time at which it has never occurred.

4.6. Human timing

Gibbon maintained an interest in human timing throughout his career. In 1969 he published an article in Science on temporal order judgments (Gibbon and Rutschmann, 1969) and wrote a comment about the problem of combining anticipation of the future with memory for the past (Gibbon, 1983). He collaborated on a chapter on infant timing (Stern and Gibbon, 1980), a review that compared Kahneman and Tversky’s cognitive model of human choice to Herrnstein’s behavior model of animal choice, and experimental studies of adult timing (Allan and Gibbon, 1987, 1994). He and Lorraine Allan collaborated on the organization of a conference on timing that brought together experts both on human timing, and timing by other animals (Gibbon and Allan, 1984). This conference undoubtedly contributed to the increasing tendency to use similar procedures for similar problems, and to explain the results using similar quantitative theories. The human temporal bisection experiment by Allan and Gibbon (1991) is an excellent example of regular results supportive of scalar timing (bisection at the geometric mean, and superposition when time was scaled in relative units). (See Fig. 6.)

These results could be accounted for in terms of a simple version of scalar timing theory with only two free parameters (clock speed and threshold). A subsequent experiment of human temporal bisection with different stimulus modalities (auditory and visual) led to hypotheses of mixing of
temporal memories (Penney et al., 1998). The memory mixing ideas were important in his interpretations of some experiments in neuropsychology.

4.7. Neuropsychology

The final field to which Gibbon devoted himself was neuropsychology, particularly the study of timing by individuals with Parkinson’s disease. He developed an interest in the biological basis of timing behavior, collaborated in a study of the effect of a dopamine agonist on response rate and timing in the rat (Ohyama et al., 2000), and he and his colleagues wrote several articles on the neural basis of timing (Gibbon et al., 1997b; Malapani et al., 2002; Gibbon and Malapani, 2002). With colleagues he developed a good reference procedure for peak-interval timing in humans (Rakitin et al., 1998). This procedure was used with cerebellar patients (Malapani et al., 1998a) and with Parkinson’s patients either ‘on’
or ‘off’ their levodopa plus apomorphine medication. When on the medication they were able to respond accurately at the two times that had been previously presented (8 and 21 s); but, when off the medication, the times of the responses migrated toward each other (Malapani et al., 1998b). This phenomenon was interpreted in terms of a memory mixing model that includes consideration of the dopamine system and an information-processing model of temporal memory Malapani and Gibbon (2002).

4.8. Other

Of course, a few Gibbon’s publications did not fit the neat outline of scalar timing theory and its applications. These include a series of articles with Don Hutchins on determinants of fetal development (Hutchins and Gibbon, 1970; Hutchins et al., 1973; Hutchins et al., 1975). He also published an apparatus article based upon the equipment he used regularly in the laboratory (Cooper et al., 1988).

5. Concluding remarks

This overview of the published research of John Gibbon is a tribute to him and his research accomplishments, and not an historical or critical review. It does not, for example, describe the influences of the research of others on his research. These influences were substantial as he indicated implicitly by his extensive lists of references, particularly in review articles, and explicitly in a review of scalar timing theory (Gibbon, 1991). He did not just use the hypotheses and conclusions of others; he was greatly affected by the quantitative results that they reported, as indicated by his secondary data analysis. He collaborated not only with students but also with many established researchers who published with him for periods of 5–20 years (Lorraine Allan, Peter Balsam, Dani Brunner, Russell Church, Stephen Fairhurst, C. R. Gallistel, Charles Locurto, Chara Malapani, Warren Meck, and Herbert Terrace). His unique approach is clear not only in the 14 articles on which he was sole author, but also in all of his collaborative efforts.

He truly enjoyed the social interactions that were an integral part of his process of doing research. He and his collaborators often engaged in discussions over periods of many months or several years. The discussions could be held in an office, a laboratory, at a scientific meeting, a restaurant, or a home. These discussions usually had a clear purpose that had been developed in advance, and he regarded his collaborators as teammates with a common goal. The successful discussions led to the development of novel ideas, and the identification of problems that were sufficiently difficult to be interesting, but which could be solved with some time, effort, and creativity. Sometimes the solution required mathematical analysis, and he was particularly productive when he had the opportunity to avoid all distractions, as when he traveled by train. He did this work on legal-sized paper, and he communicated the results to his collaborators in carefully constructed letters, and in less formal email. He had an aesthetic appreciation of simple behavioral regularities, common features of apparently unrelated theories, and challenging derivations that led to simple mathematical expressions.

Of course, there have been criticisms of scalar timing theory and its applications. The theory has been criticized for being too cognitive, for having too many parameters, for not fitting data from many procedures, and for other reasons. He defended the theory with passion, once writing ‘The critique is generally flawed, both factually and logically’ (Gibbon, 1999, p. 272). Scalar timing theory has also been praised for being clear and precise, although such characteristics made it easier to identify its flaws.

Probably the long-term influence of John Gibbon on the understanding of interval timing will not be due to the details of scalar timing theory, but will be instead due to his approach to the study of interval timing. He identified principles of interval timing that were quite general across procedures and species, such as proportional timing, constant coefficient of variation, and superposition. He identified the multiple sources of variability in perception, memory, and decision that were present in timing tasks. Then he developed a fully-specified quantitative theory that
could account for the observed data. He examined data from many species under many experimental procedures that he and his colleagues conducted, and he also made effective use of data from other laboratories. His working hypothesis was that all animals, including humans, used the same mechanisms for whatever they timed, and that timing was an essential feature of nearly everything they did.

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