Reflections on Adaptive Behavior

Essays in Honor of J. E. R. Staddon

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1 Theoretical Behaviorist: John E. R. Staddon

Nancy K. Innis

John Staddon—theoretical behaviorist. In the tradition of behavior analysis this appellation might be considered an oxymoron. However, "[e]xperimental analysis *by itself* can never make sense of behavior. Theoretical imagination is also required." (Staddon 1999, pp. 218–219) "*Conjecture*, not just about variables but also about *processes*, is essential." (Staddon 2001a, p. xi) John Staddon's theoretical imagination has set him apart from contemporary animal learning researchers. Who else would characterize his model as a leaky bucket?

Staddon's long career has been devoted to the study of the adaptive function and mechanisms of learning. His epistemological approach, theoretical behaviorism, consists in applying parsimonious black-box models to unravel the principles of learning. In doing this, he has typically taken positions that deviate from the norm. At a time when psychologists were maintaining their distance from behavioral biology, Staddon was promoting optimality theories and urging cooperation between ecologists and psychologists. (See Staddon 1980a.) Now optimality theories in psychology are commonplace. At a time when identifying mechanisms is considered the only legitimate approach to explaining behavior, Staddon is not afraid to invent functional models. At a time when physiological instantiation is the holy grail, Staddon postulates internal states that are purely theoretical.

In his most recent book, *Adaptive Dynamics: The Theoretical Analysis of Behavior* (2001a), Staddon presents theoretical behaviorism in its most recent incarnation and describes research problems to which his models have been applied, including habituation, feeding regulation, choice, spatial search, and timing. Several of the chapters in this present volume, by his former students and colleagues, deal with these topics, revealing his influence on their work. I begin with a brief biography, outlining the development of Staddon's career as both a scientist and a teacher.

Family Background and Education

John Eric Rayner Staddon was born March 19, 1937 at Lavender Cottage in Grayshott, Hampshire, England, the first child of Leonard John (Jack) Staddon and Dulce Norine Rayner Staddon. A sister, Judy, was born four years later. Jack Staddon was a Cockney, born in West Ham, who left home early and joined the army. He was stationed in India and in Rangoon, where he met Dulce Rayner. Dulce was born and grew up in a small village in Burma, although her mother's family was originally from Calcutta. After their marriage, the Staddons settled in England, and were living near Jack's base in Hampshire at the time John was born. Toward the end of 1937 they moved to London, eventually to a house in Cricklewood, an area of northwest London. During most of John's early childhood England was at war, and on more than one occasion, when the bombing became intense, he was sent to live in the country. His father was away much of the time, and from 1942 to 1944 was stationed in India with the Intelligence Corps in Karachi. His mother contributed to the war effort as personal secretary to Sir John Pratt in the Far East Section of the Ministry of Information. John's grandmother, Irene Rayner, to whom he was closely attached, lived with the family and cared for the children.

Growing up in the house in Cricklewood, John was a happy, quiet child who liked to collect "creepy crawlies" and examine them under his microscope—a pastime similar to one that Charles Darwin, one of John's academic heroes, engaged in during his youth. John was also very keen on tropical fish and at one time had six tanks. These interests continued into adulthood; John often has a fish tank at home, and he has a small collection of beautiful old microscopes. As a teenager, he liked to read science fiction, play tennis, and listen to music. Later, when he was at university, he enjoyed riding around the countryside on his Vespa motor scooter.

Early Education

Education was especially important to Dulce Staddon, and the family never scrimped on books. Both she and John's grandmother always read to the children when they were young, and John was reading on his own by the time he was four. After the war, John attended Burgess Hill School in Hampstead where his best friend was Martin Bernal, now famous for his revisionist history *Black Athena*. This was a progressive school suggested by John's uncle, Eric Rayner. At the time Rayner was night editor of the *Daily Telegraph* newspaper, and he later worked for the BBC overseas service. Over the years, to some extent, John followed in his uncle's journalistic footsteps. As an undergraduate he wrote film reviews for the university newspaper, and later he edited Duke University's faculty newsletter for a few years (1991–1994). His interest in writing for a general audience is also evident in two books, *Behaviorism: Mind, Mechanism and Society* (1993a) and *The New Behaviorism: Mind, Mechanism and Society* (2001b).

In 1947, John was 10 years old and would soon face the 11 Plus examinations, which at the time determined the type of secondary school education (grammar, technical, or secondary modern) for which a child in Britain was eligible. Realizing that the Burgess Hill School was not good academically, his mother looked for an alternative. In September 1947, John was enrolled at St. Marylebone Grammar School, a well-established grammar school for boys located near Baker Street, a 3-mile bus ride from his home. When he started at St. Marylebone, John was at something of a disadvantage because he had declined to be exposed to any mathematics at the progressive school. However, within a few months, with the help of a tutor, he had mastered the subject. John completed his elementary and high school education at the St. Marylebone Grammar School.

Undergraduate Years

John enrolled at the University of London in 1955. For his A levels, which qualified him for university, he had specialized in pure and applied mathematics, physics, and chemistry. He started out in engineering. Before long, however, he realized that he could switch to psychology, which was closer to biology, the subject to which he "had been devoted since youth" but had been unable to study at St. Marylebone because the school lacked the necessary facilities (Staddon 1991, p. 1). After two years at university and feeling somewhat jaded, perhaps because he was not making the most of his academic opportunities, John interrupted his studies and joined his parents, who were living in Northern Rhodesia (now Zambia). In Rhodesia he worked for the World Health Organization in a nutrition program. On a trip into the wilderness to collect blood samples, he became very ill, likely with malaria, and would have died had it not been for an observant nurse who recognized his symptoms and obtained the appropriate medication. Returning to England, John completed his undergraduate program and graduated with a B.Sc. in Psychology from University College, London in 1960.

John's record at London was not outstanding, yet graduate school was an obvious choice for someone with an inquiring mind. Through their advertisements on bulletin boards at the University of London, he was attracted to universities in North America. Accepted by all three departments to which he had applied, he chose Hollins College, a small school in Roanoke, Virginia, where he spent a year in the graduate program. His intellectual ability soon became obvious to his professors at Hollins. They encouraged him to apply to Harvard University, and he left Hollins College without completing the master's program.

Graduate School—Harvard University

John Staddon arrived at Harvard in September 1961 and joined a group of dedicated researchers in B. F. Skinner's Pigeon Lab located in the basement of Memorial Hall. His faculty supervisor, Richard Herrnstein, had earned his doctorate under Skinner only 6 years earlier. Most of Herrnstein's students were doing research on choice—this was the year that he introduced the Matching Law, and so John, never the conformer, decided to work on something else. Because of the ubiquity of temporal processes in both classical and operant conditioning, he chose to study temporal discrimination, believing that "understanding the mechanism of timing might provide a key to understanding conditioning in general" (Staddon 1991, p. 1).

Most of the timing experiments John carried out at Harvard involved differential reinforcement of low rate (DRL) schedules of reinforcement. On these schedules, an animal must wait a specified time (DRL value) before making a response in order to receive a reinforcer. In the experiments. His doctoral dissertation, "The effect of 'knowledge of results' on timing behavior in the pigeon," involved experiments in which the DRL value changed cyclically every 5 minutes. A limited hold was added so that the birds were required to respond at times demarcated by both an upper and a lower time limit. The major variable examined was the effect of feedback stimuli, indicating to the bird that it had waited too long before pecking (a brief flash of red light on the key) or not long enough (a flash of green light). The birds showed an ability to track the changing time requirements; however, although knowledge of results improved performance, especially for birds that were not timing well, probe tests showed that it was not the information of too long or too short, but rather the relative frequency of the feedback stimuli, that seemed to control behavior (Staddon 1963). In a reflective comment on his study, Staddon observed:

> The interesting things about this dissertation are of course that (a) the hypothesis to be tested—"knowledge of results"—was cognitive, not at all something that could be inferred from standard conditioning principles; and (b) the results showed it to be wrong. But cognitive ideas about animal behavior, like deleterious recurrent mutations, just keep coming back, only to be refuted almost every time. (J. E. R. Staddon, personal communication, June 2, 2003)

In those days experiments were controlled by electro-mechanical equipment, and wiring the complex DRL program for these studies was "a technical *tour de force*" (Staddon 1991, p. 1). John completed the work for his doctorate by the end of 1963, and received his Ph.D. in experimental psychology from Harvard in 1964. His dissertation research was published in the *Journal of the Experimental Analysis of Behavior* (*JEAB*) in an article dedicated to B. F. Skinner in his 65th year (Staddon 1969a).

The ambition of most young scientists in the 1960s (perhaps even today) was to have a paper published in the prestigious journal *Science*. John Staddon's first academic publication appeared in *Science* in 1964. Following up on the problem of temporal tracking addressed in his doctoral research, he devised a simpler procedure in which pigeons were exposed to a cyclically changing fixed-interval (FI) schedule. Interval durations changed according to a sinusoidal pattern which offered the possibility of applying a linear systems analysis. On this simpler cyclic schedule, pigeons' response rates tracked the changes in inter-reinforcement time, but were out of phase with the schedule cycle; rate was highest when there were fewest reinforcements (Staddon 1964). In most of his subsequent research on timing, Staddon would use variants of a cyclic FI procedure. (See below.)

Living in Cambridge, Massachusetts, John was able to take advantage of opportunities to explore areas of psychology beyond the Pigeon Lab. He was exposed to the field of visual perception when a research assistantship with Jacob Beck provided financial support during his first term at Harvard.

He also carried out neurological research on crayfish in Larry Stark's Electronic Systems Laboratory. An entirely different perspective was obtained when, along with fellow graduate students Jacques Mehler and Charlie Harris, John participated in some of the activities at the Center for Cognitive Studies, recently established by George Miller and Jerry Bruner. In retrospect, however, the most significant experience was a course on artificial intelligence that he attended at the Massachusetts Institute of Technology. The course, developed by Marvin Minsky, was taught that year by John McCarthy. Minsky's notes for the course were later published in the book *Computation: Finite and Infinite Machines* (Minsky 1967). If this course did not directly influence the way Staddon began to formulate his approach to understanding behavior, it certainly was compatible with it. In a brief mimeographed paper dated 1963, the outline for a presentation at Skinner's graduate seminar, John proposed "a simple-minded formalism for talking about behavior." The proposal began as follows:

> An organism both acts upon the environment and is acted upon by it. What is the simplest formalism that will take account of this fact? The following is offered as a possible (by no means original) candidate, in the hope that it constitutes a language in which may be expressed all and only meaningful (testable) statements about behavior. Since it is probably not adequate, its real purpose must be to encompass its own destruction by yielding something more satisfactory. . . . An organism is considered as a black-box or machine and by convention is described in terms of three constructs: *input* (I), *output* (O), and *internal state* (S). . . . (Staddon 1963, pp. 1–2)

In this outline we find several of the core elements of the theoretical framework that Staddon has embraced throughout his career. First, look for simple (parsimonious) explanations; second, develop "black-box" models of behavior that include consideration of the internal state of the system; third, recognize that all theories are temporary, eventually to be replaced. John recalls that "Skinner was unimpressed and uninterested" (personal communication, June 2, 2003).

Academic Career

University Appointments

In 1964, John Staddon accepted an appointment in the Psychology Department at the University of Toronto, and he and his first wife, Nada Ballator, whom he had met at Hollins College, moved to Toronto. It was here that their son, Nicholas, was born the following year. A second child, Jessica, was born in Durham, North Carolina in 1969. At Toronto, Staddon for the first time was faced with teaching undergraduate students. In a course on experimental psychology (Psychology 91) he spent considerable time discussing the black-box systems approach that he believed to be the best way to attain an understanding of behavior. The undergraduates were baffled. By early 1965, Staddon had several experiments up and running in the sub-basement of Sidney Smith Hall where the psychology animal laboratories were located. These included studies of timing (involving both DRL and FI schedules), choice, and, before long, the "frustration effect." The following year, he began reexamining Skinner's "superstition" experiment. Staddon's research program, initiated at Toronto and continued at Duke University, will be examined in detail in later sections of this chapter.

Perhaps more than anything else, the interminable winters in Ontario encouraged the Staddons to move back to the South. In 1967, John joined the faculty of the Psychology Department at Duke University in Durham, North Carolina, where he moved quickly through the ranks, becoming a full professor in 1972. In 1983 he was named James B. Duke Professor of Psychology. In addition, he was appointed professor of zoology in 1979 and professor of neurobiology in 1988. From 1985 to 1987, he was chairman of Duke's psychology department. Over the years, he has served on many university-wide committees. In 2002 he was appointed secretary of the Faculty Council.

Editorial Work

Staddon has contributed to psychology as an editor of several journals. In 1979, he joined Chris Bradshaw as US editor of *Behaviour Analysis Letters* (*BAL*), a journal that typically published short accounts of recent research. In 1983, *BAL* amalgamated with *Behavioural Processes* (*BP*). John continued as co-editor of *BP* until 2001, when Clive Wynne took over from him. Wynne (chapter 11), a research collaborator who was at one time a postdoctoral fellow in Staddon's lab, thus provides a continuity of perspective for the journal. In 1991, Staddon joined the editorial board of *Behavior and Philosophy*, taking over as editor of that journal in 1996. Over the years he was frequently on the editorial board of *JEAB*, and he served as associate editor from 1979 to 1982. He has served on the editorial boards of several other journals, including *Behaviorism* and the *Journal of Experimental Psychology: Animal Behavior Processes*.

Leaves and Awards

Throughout his career various awards have permitted Staddon to spend time in psychology departments in several countries; he has visited or held positions in departments in Australia, Brazil, England, Germany, Italy, and Mexico. John chose to spend his first sabbatical leave (1973–74) working with David McFarland, a member of the Animal Behavior Research Group at Oxford University. John had been interested in McFarland's work for some time, believing that "sophisticated feedback analysis [was] possibly a better way to handle the complexities of behavior on reinforcement schedules than the rather crude descriptive principles then current" (Staddon 1991, p. 4). At Oxford he also got to know many of the people who, during the next decade, would become leading figures in behavioral biology as optimality approaches to foraging behavior became popular. One of these individuals was Alasdair Houston, who was an Oxford undergraduate at the time. Houston would later spend a year at Duke in Staddon's lab.

On the invitation of Arturo Bouzas, Staddon spent several weeks at the Laboratorio de Analisis Experimental de la Conducta (Laboratory of the Experimental Analysis of Behavior) in Coyoacan, Mexico in 1981, the year in which he held a Guggenheim Fellowship. In 1985, he received the Alexander von Humboldt Prize, an award that allowed him to spend 1987–88 in Juan Delius's laboratory in Bochum, Germany. This proved to be a very happy year as John recovered from trying times, both personally and as department chair, in the company of Lucinda Paris, his second wife. Follow-up visits to Delius's laboratory, which had moved to the University of Konstanz, were also supported by the Humboldt Foundation.

John's association with the Brazilian psychologist Jose Lino Oliveira Bueno began in 1986, when Bueno invited him to visit the University of São Paulo in Riberão Preto. Other visits to Brazil followed, including one as a Fulbright Distinguished Scholar in 1989. In 1988 Bueno spent a sabbatical year at Duke in Staddon's laboratory. In 1991, Staddon was invited by Giulio Bolacchi (chapter 15) to take part in the Associazione per l'Istituzione della Libera Università Nuorese (Association for the Institution of a

Free University in Nuoro), and every year since then he has spent a week in Sardinia participating in this program. From 1995 to 2000, Staddon held the position of adjunct professor at the University of Western Australia in Perth. He visited that department on two occasions to collaborate with Clive Wynne, who was on the faculty there. They co-edited a book, *Models of Action: Mechanisms for Adaptive Behavior*, which was published in 1998.

Staddon is a fellow of the New York Academy of Sciences, of the American Psychological Society, and of the American Association for the Advancement of Science. He is a member of the Society of Experimental Psychologists and a Trustee of the Cambridge Center for Behavioral Studies.

Theory and Research

Philosophy of Science

Although he received his graduate training at Harvard, the bastion of Skinnerian behaviorism, Staddon did not adopt the atheoretical position to which most behaviorists subscribe. Early on, he pointed out the danger in claiming to reject theory, suggesting that "those who ignore their metaphysical preconceptions are liable to be misled by them" (1969b, p. 484). In a review of Floyd Ratliff's book *Mach Bands*, he praised the virtues of "speculative thought" and "Mach's view of the proper role of theory" (Staddon 1969b, p. 485), which involved "a formula which represents the facts more concisely and plainly than one can with words, without, however, claiming quantitative exactness" (Ratliff 1965, cited in Staddon 1969b, p. 485). Staddon's models are quantitative and they are formal (theoretical). He takes the position that a model need not be isomorphic with physiological processes as long as it can lead to explanation and understanding. The best theories are, of course, parsimonious and capable of accounting for many phenomena. We can see this approach to theory exemplified in many of the models that Staddon has introduced throughout his career, including those presented in *Adaptive Dynamics*. And these will not be the last models from Staddon's pen. It is his belief that theories are ephemeral; they must be constantly under revision. His hope is that "as each model is proposed and, eventually, retired, we may learn a little more about the essential mechanisms of learning—so the next model may be a little bit better, a little bit more securely founded" (Staddon 2001a, p. xi).

Research Program

Temporal Control of Behavior At Toronto, Staddon continued his research on the DRL performance of pigeons, using veteran birds he had brought with him from Harvard. After several publications appeared with the same subject numbers, colleagues began to chide John, asking him why he couldn't afford to get new birds. Indeed, most of his experiments did not require naive subjects, and both rats and pigeons from the Toronto laboratory, including some of the old Harvard birds, went along when Staddon moved to Duke. A survey of his *JEAB* publications of the late 1960s and the early 1970s will reveal the identities of the stalwart pigeons who served in these studies.

Most of Staddon's research on temporal discrimination at Toronto and during his first few years at Duke involved cyclic FI, rather than DRL, schedules. On simple FI schedules, animals typically pause a constant proportion of an inter-food interval before starting to peck the response key. Post-reinforcement pause, a more direct indicator of temporal control, soon replaced response rate as the main datum of interest in the cyclic studies. Changes in pause track changes in the input cycle directly, rather than out of phase as is the case with the response-rate measure. In the first doctoral dissertation supervised by Staddon, Nancy Innis showed that pigeons could successfully track intervals of seven different durations which increased and then decreased across a cycle according to an arithmetic progression (Innis and Staddon 1971). The results of these experiments, and other studies involving schedules with fewer intervals per cycle, identified the conditions under which temporal tracking did or did not occur. However, no progress was made at identifying the mechanism of temporal control. At the time, when computers were not a standard tool in psychology laboratories, data analysis was laborious, simulations were difficult, and so model development was limited.

Working with FI schedules led Staddon to a tangential foray into an area generally associated with runway, rather than Skinner box, research. Just down the hall from his lab at Toronto, John's senior colleague Abe Amsel was studying the "frustration effect." The procedure involved recording the speed at which rats ran down two consecutive runways. There was always food in the goal box at the end of the second runway, whereas the goal box at the end of the first runway contained food on only 50 percent of the trials. Running speed in the second runway was substantially elevated followed non-reward in the first goal box. Amsel attributed this increase to heightened motivation due to frustration on not receiving food; hence the term "frustration effect." Staddon's work with FI schedules led him to suggest a simpler explanation. In an analogy to the double-runway situation, he set up a study in which birds were exposed to pairs of fixed intervals. Reward always was presented for a peck at the end of the second interval; however, it was available after only 50 percent of the first intervals of a pair. Non-rewarded intervals terminated in a time out. Response rate was much higher in intervals that were preceded by non-reward (N) than by those preceded by reward (R). Staddon concluded that this elevation in rate was the result of the absence of inhibitory after-effects of reinforcement, an "omission effect," and that a similar explanation could account for the increase in running speed after non-reward in Amsel's studies (Staddon and Innis 1969).

In subsequent studies at Toronto and at Duke, Staddon further delineated the inhibitory properties of reinforcement and stimuli associated with it. On FI schedules it is, of course, adaptive for the animal to refrain from responding early in intervals when food is never available. Thus, animals attend to and recall cues that allow them to predict food availability. John Kello (chapter 14) carried out omission-effect studies for his doctoral research at Duke in the early 1970s. (See appendix.) In a 1974 article in the *Psychological Review*, Staddon outlined his ideas on the role of memory and attention in timing, emphasizing that inhibitory temporal control by a time marker (e.g. reward) is "a function of the whole preceding temporal context" (p. 376). Like stimulus control in other situations (e.g. matching-to-sample studies), temporal control is determined by the value of the stimulus, retrieval cues, and interference or confusion effects. The omission effect, then, could be the result of confusion as to which stimulus came last (R or N), could be a memory effect, or could be due to overshadowing by attention to the salient stimulus (R).

Interest in timing research took a back seat for over a decade, but in the late 1980s, with the aid of computer models, theoretical progress was at last possible. In part, Staddon was stimulated to return to studies of timing because he saw a number of flaws in the popular scalar expectancy theory (SET) being advanced by John Gibbon, Russell Church, and their associates (Gibbon 1977; Gibbon and Church 1981, 1984). In collaboration with post-doctoral fellows Jennifer Higa and Clive Wynne, research on cyclic schedules was resumed and a series of models of timing advanced. The first experiments were carried out when Staddon was on leave in Bochum. During the previous few years, he had been working on optimality models of choice behavior. (See below.) Now he devised a simple procedure to extend his optimality analysis to temporal discrimination. Wynne, who was also interested in issues of reinforcement maximization having just completed doctoral research on momentary-maximizing explanations of choice at the University of Edinburgh, was happy to collaborate. The procedure, a response-initiated delay (RID) schedule, is as follows: after reinforcement the bird is presented with a red key light; the first peck on the red key changes its color to green and after a fixed time (T) reinforcement occurs, independent of the bird's behavior. The optimal strategy, of course, is for the bird to peck the red key as soon as it comes on. However, birds do not do this; they wait for a period of time (t) before pecking. The duration of this wait time is linearly related to the duration of the inter-food interval ($t + T$). Moreover, Staddon and Wynne found that "the timing process seemed to be both *rapid* and *obligatory*, i.e. the animals were evidently constrained to behave in this way" (Staddon 1991, p. 9). These results suggested that interval timing involved a "one-back" mechanism they called linear waiting (Wynne and Staddon 1988). Support for linear waiting came from experiments carried out with Jennifer Higa (Higa 1996; Higa, Wynne, and Staddon 1991). For example, using a RID schedule in which a single, short "impulse" interval was interpolated into a series of longer intervals, they found that pigeons' wait times were short in the interval following the interpolated interval, but only in that interval.

Over the next few years, Staddon and Higa continued to develop other timing models. The first of these was a model in which post-reinforcement events were seen "to be represented dynamically by a diffusion-like memory process" (Staddon 1991, p. 10). This diffusion-generalization model (which represents time spatially) was developed at the time Staddon was working with Alliston Reid (chapter 3) on a diffusion-generalization model to account for spatial navigation. Tolman's (1948) idea that rats have a cognitive map of their environment, for example of the location of food on a maze, was criticized because he offered no mechanism for reading the map. The model of Reid and Staddon (1997, 1998) provided a mechanism—an associative process based on stimulus generalization (essentially a similarity space). In the diffusion-generalization model of timing (Higa and Staddon 1997), reinforcement augments "activation at a point whose distance from the origin is proportional to time elapsed since the time marker (reinforcer delivery . . .). Activation diffuses constantly in real time" with rate of responding "represented by the height of the activation surface at each instant of time in the to-be-timed interval" (Staddon, Chelaru, and Higa 2002a, p. 106). In one version of the model, responding was based on a gradient of activation and a threshold. These models had some difficulties; for example, it was not possible to duplicate the performance observed on cyclic-interval schedules or capture all the features of dynamic timing effects.

Scalar expectancy theory assumes, *a priori*, that timing depends on a biological clock. Staddon maintains that "*there may be no separate 'internal clock'* at all; . . . interval time discrimination is just like any other discrimination," and that animals remember the occurrence of salient time markers and learn "to discriminate between memories of different ages, and thus of different 'strengths'" (2001a, p. 338). Moreover, in most versions of SET time is represented linearly (proportional timing) and the decision whether or not to respond is determined by the ratio of the representations of time in working and reference memory. Staddon's position is that time is encoded in a log-like manner and that there is a constant-difference response rule. There is good evidence for this with interval schedules; for example, a power function relationship between post-reinforcement pause and interval duration has been shown to hold for performance on both simple FI and cyclic FI schedules (Innis and Staddon 1971). Both linear and non-linear models make the same prediction for simple FI schedules. However, SET cannot account for temporal tracking on cyclic schedules.

Power functions are not the only non-linear functions, and Staddon's most recent model is multiple-time-scale (MTS) theory (Staddon and Higa 1999; Staddon, Chelaru, and Higa 2002a). This model combines linear waiting with a short-term memory model originally devised to account for rate-sensitive habituation (Staddon 1993b; Staddon and Higa 1996). In the habituation model the strength of the fading stimulus trace is represented by the output of a set of cascaded leaky integrators (the leaky bucket analogy). The integrator model has also been applied to the dynamics of feeding behavior. Although "behavioral theories stand on their own feet" and are "valid to the extent that they describe behavioral data accurately and economically" (Staddon 2001a, pp. 150–152), it is encouraging to find agreement with physiology. Recently a physiological counterpart of the cascaded integrators idea has been reported for the human visual system (Glanz 1998).

For timing, the integrator model says that "what is learned on periodic schedules is the reinforced and non-reinforced values of the animal's memory trace for the time marker" (Staddon 2001a, p. 341). In line with the approach to research that has guided him throughout his career, Staddon starts by making "qualitative (rather than quantitative) predictions from a theory that uses as few theoretical concepts as possible" (Staddon and Higa 1999, p. 247), looking at its application across a broad range of a situations involving individual subjects rather than group averages. MTS theory can account for a wide range of data from a variety of studies on temporal control. Both Jennifer Higa (chapter 8) and Mircea Chelaru (chapter 9) report related research on timing in this volume.

In the early 1980s, most psychologists, it seemed, were in agreement that scalar expectancy theory could account for interval timing. Then John Staddon began to develop his dynamic models of timing, reactivating many of the issues surrounding temporal control and forcing SET theorists into controversial debate. For example, *JEAB* devoted a large section of an issue to an article by Staddon and Higa (1999) and commentaries on it. Staddon's models are now receiving increased attention and are stimulating research that will finally help us explain how animals time, a process so integral to an understanding of all conditioning processes.

Biological Constraints on Learning Curiosity is the hallmark of a good scientist. Staddon was curious about (perhaps suspicious of) the results reported in a widely cited article by Skinner on "superstitious" behavior in pigeons. Skinner (1948b) reported that pigeons exposed to periodic free presentations of food (a fixed-time (FT) schedule) were observed to display idiosyncratic responses during inter-food intervals. Skinner believed that these responses were the result of the strengthening action of reinforcement and that the experiment provided support for his general-process theory of learning. Staddon took his cue from the ethologists and decided to make detailed observations of what the birds were doing throughout the inter-food interval. Virginia Simmelhag, who was an undergraduate student in one of his courses at Toronto at the time, took on the tedious task of recording the second-by-second behavior of pigeons exposed to such FT schedules. She later completed her master's degree at Toronto on this project. (See appendix.)

The data provided evidence that the behavior occurring just prior to food presentation was not an idiosyncratic response, strengthened by reinforcement, but rather a food-related (pecking) response. Immediately following reinforcement the birds engaged in other, more idiosyncratic behavior. Staddon and Simmelhag (1971) identified two behavioral states associated with these two types of responses, which they labeled interim and terminal. The editor of the *Psychological Review*, where the article reporting these data was submitted, asked Staddon to expand on the brief theoretical account drawing a parallel between operant conditioning and Darwinian selection that they had presented, and he was happy to comply. The published article, which has become a classic, includes an account of many conditioning phenomena within the variation-selection theoretical framework. As well as superstitious behavior, they dealt with classical and instrumental conditioning, the recently reported phenomenon of autoshaping, and a number of schedule-induced behaviors such as polydipsia. The article was received very well and became part of a growing body of findings reporting constraints on learning.

The "superstition" research led Staddon and his students to conduct a number of studies examining schedule-induced behavior, including a doctoral dissertation by Alliston Reid. (See appendix.) In collaboration with Sandra Ayres, a master's student at Duke, Staddon looked at how animals distributed their time among a number of activities during inter-food intervals, when opportunities for several other behaviors were made available. These data allowed him to develop a theoretical account presented in a chapter in *The Handbook of Operant Conditioning*, a book he co-edited with Werner Honig (Honig and Staddon 1977). As well as pointing out that the various behaviors reflect different internal states, Staddon (1977a) emphasized the idea that there was competition among them. A few years later, he developed a model for instinctive drift, the finding that a well-learned operant response to obtain food may begin to deteriorate and be replaced by innate food-related behavior (Breland and Breland 1961). Based on the idea of reciprocal inhibition between competing (incompatible) behaviors, the model is able to predict a change from an operant response to a species-specific behavior (Staddon and Zhang 1991).

Staddon's research on schedule-induced behavior played an important role in advancing the changing conception of both operant and classical conditioning that was emerging during the 1970s, a movement away from the "naive reflexology" that had dominated learning theory during the preceding decades. The results reported by Staddon and Simmelhag (1971) indicated that classical conditioning is "an integral component of the 'variational' mechanisms which allow organisms to generate adaptive behavior in advance of instrumental contingencies" (Staddon 1991, p. 2). Along with other research published at the time (see Shettleworth 1972), this study helped advance the view that there are biological constraints on learning which cannot be ignored. At last psychologists and biologists were talking to one another, and John Staddon was a key figure in bringing about this change.

Optimality and Choice John Staddon was introduced to theoretical accounts of choice behavior when he was a graduate student at Harvard. At the time, Richard Herrnstein was developing his matching law, which describes the fact that in choice situations, such as concurrent reinforcement schedules, animals will match their relative rate of responding to the relative reinforcement rate (Herrnstein 1961). However, Staddon's long-time interest in biology, and the view that animals behave adaptively, led him to develop a theoretical analysis of choice responding based on utility theory. In fact, he first proposed an expected utility model for choice in an article submitted to *JEAB* in December 1967. The reviewers were not persuaded by his theoretical ideas which they considered too speculative and not particularly relevant to the data from the study he was reporting, an experiment involving DRL schedules. They rejected the paper. The data were finally published, sans utility theory, the following year (Staddon 1968). However, stimulated by his interactions with the behavioral ecologists at Oxford during his sabbatical year, John continued to "mull over the relationships between operant conditioning and behavioral ecology" (Staddon 1991, p. 5). Applying optimality theory to the matching law, he suggested that matching could be the result of reinforcement rate maximization and was able to show this for a class of feedback functions (Staddon 1980b). In an effort to make researchers aware of the "intimate relation between the concepts of utility, reinforcement, and Darwinian fitness" (Staddon 1980a, p. xviii), Staddon brought together contributions by economists, psychologists, and behavioral ecologists in an edited volume, *Limits to Action: The Allocation of Individual Behavior*. The result was to facilitate communication between ecologists and psychologists leading to many productive collaborations.

In what he referred to as "a first step on what is likely to be a long and theoretically involved journey" (Staddon 1979a, p. 2), Staddon published his own optimality theory of behavioral allocation, known as the minimum-distance model (Staddon 1979b). This model assumes that animals "optimize not a single variable ... but rather some function of the total repertoire of behavior, subject to limitations of time and the constraints imposed by the schedule" (ibid., p. 50). Attempting to maintain the preferred level of the various activities in this repertoire under schedule constraints, they will act to "minimize the deviation" from the preferred distribution. The minimum-distance model proved successful in explaining a large number of the properties of molar behavior observed on schedules of reinforcement.

John Staddon's contributions to the study of variability and choice has been wide ranging, stimulating research and theory development by both colleagues and competitors. His elegant minimum-distance model has implications, not only for the evolution and ecology of learning, but also for neuroscience. In collaboration with a number of graduate students he has contributed to the real-time analyses of choice behavior in a number of areas; for example, studies of ratio invariance with John Horner (chapter 13), of momentary maximizing with John Hinson, and of history effects on choice with Derick Davis. More recently, in collaboration with his Duke University colleague Dan Cerutti (chapter 6), Staddon has been looking at models of choice that emphasize time to reinforcement as the important factor in determining preference in animals. This emphasis on the ubiquity of temporal processes in learning phenomena has been a consistent element of Staddon's conception of what controls animal behavior throughout his career.

Principles of Learning

John Staddon's books have presented a fresh and reasoned perspective on experimental psychology. In 1983 he published a textbook, *Adaptive Behavior and Learning*, that emphasized theoretical principles of learning rather than experimental techniques or findings. Moreover, unlike most learning theorists who operate on the premise that to be scientific one must only consider mechanistic accounts, he promoted explanations "in terms of outcomes, either evolutionary outcomes (Darwinian fitness) or outcomes in the life of the individual (goal or motives, reinforcers or 'preference structures'—take your pick)" (Staddon 1983, p. x). This willingness to consider functional, along with mechanistic, accounts has consistently been a characteristic of Staddon's approach, rooted, of course, in his longstanding interest in behavioral biology. Then, in 2001, John brought together his most recent theoretical ideas in *Adaptive Dynamics*. This book is "an argument for a simple proposition: that the way to understand the laws and causes of learning in animals and man is through the invention, comparison, testing, and modification or rejection of black-box models" (Staddon 2001a, p. ix). John Staddon has spent his entire career doing just that.

I first met John Staddon when I was "assigned" to carry out my fourth-year honors' thesis research with him at the University of Toronto. The project I had planned to do fell through and John, who had just arrived at Toronto, was looking for a student. No one had approached him initially. According to the neo-Hullians who dominated the animal labs at Toronto at the time, Staddon was a Skinnerian and doing his kind of research was to be avoided at all costs. But I soon became a devoted member of his lab, helping to set things up and enjoying the excitement of discovering how to be a researcher. Our motto in those days came from the nineteenth-century physicist Michael Faraday: "Work. Finish. Publish." John certainly continued to follow that advice.

More than 30 years later, I am grateful for the twist of fate that sent me to Staddon's lab, with its one relay rack and a few "Harvard" pigeons. Little did I know then that the young "Skinnerian," just starting his career, would become the respected scientist we are honoring now. Little did I know that, as well as mine, the lives of many students would be altered as the result of being a part of "Staddon's lab." As my teacher and mentor, John taught me how to think about research, about science—and about life. As a cherished friend, he has always been there for me over the years. Thank you, John, for giving me the opportunity to be a part of it all.

Students and colleagues who have worked in Staddon's lab remember above all the stimulating atmosphere of the weekly lab meetings. As one former student put it, John "was the creative variation that fed the selective minds of the students" (A. Machado, personal communication May 12, 2003). The following chapters reveal the evolution of those minds.

Appendix

Doctoral Dissertations Supervised by J. E. R. Staddon

Innis, Nancy K. Temporal tracking on cyclic-interval schedules of reinforcement (Duke, 1970).

Malone, John C. Contrast effects in maintained generalization gradients (Duke, 1972).

Kello, John E. Observation of the behavior of rats running to reward and nonreward in an alleyway (Duke, 1973).

Davis, J. Michael. Socially-induced flight reactions in pigeons (Duke, 1973).

Starr, Bettie C. Sensory superstition on interval schedules (Duke, 1976).

Reid, Alliston K. Schedule-induced behavior: Amount and order of activities controlled by behavior interaction (Duke, 1981).

Hinson, John M. Momentary maximizing as a basis for choice (Duke, 1981).

Motheral, M. S. Optimal allocation of behavior: Ratio schedules (Duke, 1982).

Kessel, K. Kin selection, dominance and sociality in *Lemur catta* and *Lemur fulvus*: An experimental and observational analysis (Duke, 1982).

Horner, John M. Probabilistic choice in pigeons (Duke, 1986).

Kohn, Arthur. Effect of variable reward amount and delay on repeated choices (Duke, 1989).

Davis, Derick G. S. Probabilistic choice: Empirical studies and mathematical models (Duke, 1991).

Machado, Armando. Behavioral variability and frequency-dependent selection: Laboratory studies with pigeons (*Columba livia*) (Duke, 1993).

Dragoi, Valentin. Dynamics of operant conditioning (Duke, 1997).

Cleaveland, J. Mark. The role of the response in matching-to-sample tasks using pigeons and budgerigars (Duke, 1998).

Talton, Lynn. Timing, reward and the dopamine system (Duke, 2002).

Hopson, John W. Timing without a clock: Learning models as interval timing models (Duke, 2002).

Master's Theses Supervised by J. E. R. Staddon

Innis, Nancy K. Cyclic-interval schedules: The effect of within-session experience with discriminative stimuli (Toronto, 1967).

Simmelhag, Virginia L. The form and distribution of responding in pigeons on response-independent fixed- and variable-interval schedules of reinforcement (Toronto, 1968).

Kello, John. The control of responding on cyclic fixed-interval schedules of reinforcement (Duke, 1969).

Bowen, Charles. When, where, and why of polydipsia (Duke, 1972).

Ayres, Sandra. The effect of periodic food delivery on the behavior of rats (Duke, 1973).

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