

Sensitization–Habituation May Occur During Operant Conditioning

Frances K. McSweeney, John M. Hinson, and Cari B. Cannon
Washington State University

Operant response rates often change within experimental sessions, sometimes increasing and then decreasing. The authors attribute these changes to sensitization and habituation to aspects of the experimental situation presented repeatedly (e.g., reinforcers) or for a prolonged time (e.g., the experimental enclosure). They describe several empirical similarities between sensitization–habituation and within-session changes in operant responding. They argue that many alternative explanations for within-session changes in operant responding can be dismissed. They also examine some implications of linking the literatures on habituation and operant responding. Because responding follows a similar pattern in several other cases (e.g., human vigilance, classical conditioning, and unconditioned responding), 2 relatively simple processes may be responsible for the temporal patterning of behavior in a wide variety of situations.

We observed large changes in response rate within experimental sessions when subjects (e.g., rats) responded on operant conditioning procedures (e.g., McSweeney, Hatfield, & Allen, 1990). In many of our experiments, response rates increased to a peak and then decreased. In other experiments, response rates increased without decreasing or decreased without increasing. Figure 1 contains an example of each of these types of changes. The top represents results for rats pressing levers on multiple variable interval (VI) 60-s VI 60-s schedules; the middle, the results for rats pressing levers on a VI 15-s schedule; and the bottom, the results for pigeons pecking keys on a variable ratio (VR) 15 schedule. Each graph represents the proportion of total-session responses during successive 5-min intervals in the session. Throughout this article, we calculated proportions by dividing the number of responses during a 5-min interval by the total number of responses during the session.

Although within-session changes in operant responding have been observed in the past (e.g., McSweeney & Roll, 1993), these changes have been treated as problems to control by procedures, such as giving *warmup* trials (e.g., Hodos & Bonbright, 1972) or time to adapt to the apparatus (e.g., Papini & Overmier, 1985), rather than as phenomena to study. Further consideration suggests that within-session changes deserve study in

their own right. The changes are large, orderly, and reliable (e.g., McSweeney & Hinson, 1992). They occur for a wide variety of species, procedures, responses, and reinforcers (e.g., McSweeney & Roll, 1993). They may also have a number of important theoretical and methodological implications (e.g., McSweeney & Roll, 1993). For example, within-session changes challenge both molar (e.g., Herrnstein, 1970) and molecular (e.g., Hinson & Staddon, 1983) theories. Molar theories are challenged because within-session changes imply that the primary dependent variable, rate of responding averaged over the session, used by these theories masks regularities in behavior at a more molecular level. Molecular theories are challenged because they must account for within-session changes if they are to reach their goal of describing behavior on a moment-by-moment basis.

In this article, we argue that the variables that produce the well-known phenomena of sensitization and habituation produce within-session changes in operant responding. Just as responding to a stimulus usually increases (sensitization) and then decreases (habituation) when that stimulus is presented repeatedly or for a prolonged time (Groves & Thompson, 1970), operant responding increases (sensitization) and then decreases (habituation) because some aspects of the operant procedure are presented repeatedly (e.g., reinforcers¹) or for prolonged periods (e.g., the experimental chamber).

In the first part of this article, we show that the empirical characteristics of within-session changes in operant responding are sufficiently similar to the empirical characteristics of sensi-

Frances K. McSweeney, John M. Hinson, and Cari B. Cannon, Department of Psychology, Washington State University.

This article is based on work supported by National Science Foundation Grants IBN-9207346 and IBN-9403719.

We thank K. Geoffrey White and William Palya for their advice on the mathematical modeling of the data and Shelly Berendes for her help in fitting the data. We also thank John M. Roll, Samantha Swindell, and Jeffrey N. Weatherly for their comments on an earlier version of this article. Portions of these data were presented at the May 1995 meetings of the Society for the Quantitative Analysis of Behavior and the Association for Behavior Analysis, Washington, DC.

Correspondence should be addressed to Frances K. McSweeney, Department of Psychology, Washington State University, Pullman, Washington 99164-4820. Electronic mail may be sent via Internet to fkmcs@mail.wsu.edu.

¹ Throughout this article, we argue that sensitization–habituation occurs to the reinforcers used in operant conditioning. The use of the term *reinforcer* in this context is technically incorrect. We argue that sensitization–habituation occurs to stimuli, such as food and water, that are used as reinforcers in operant situations. Technically, these stimuli need not act as reinforcers for sensitization–habituation to occur. For example, sensitization–habituation would be expected even if food or water were presented independently of responding. The term *reinforcer* is used to distinguish these stimuli from other stimuli that are also present during operant situations (discriminative stimuli, the experimental enclosure, etc.).

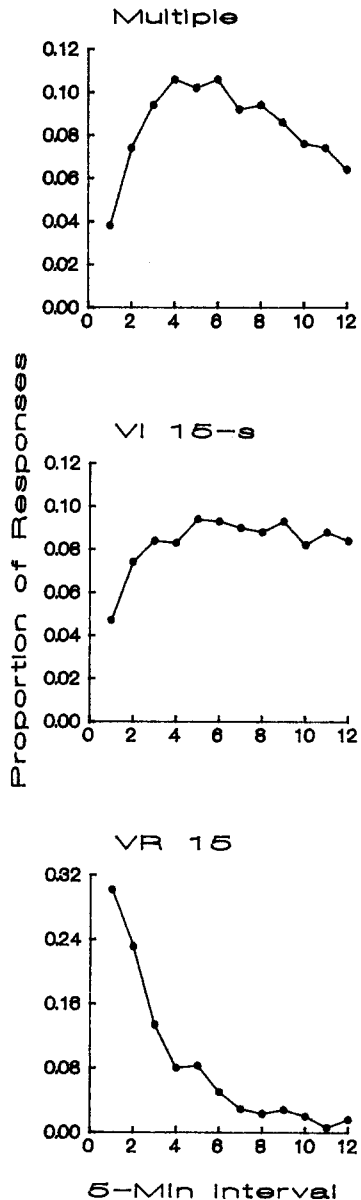


Figure 1. Proportion of total-session responses during successive 5-min intervals in the session for rats pressing levers on multiple variable interval (VI) 60-s VI 60-s schedules (top; from "Within-Session Responding as a Function of Post-Session Feedings," by F. K. McSweeney, J. Hatfield, & T. M. Allen, 1990, *Behavioural Processes*, 22, p. 182; copyright 1990 by Elsevier, Inc.; adapted with permission), for rats pressing levers on a VI 15-s schedule (middle; from "Within-Session Changes in Responding During Variable Interval Schedules," by F. K. McSweeney, J. N. Weatherly, & S. Swindell, 1996, *Behavioural Processes*, 36, p. 72; copyright 1996 by Elsevier, Inc.; adapted with permission), and for pigeons pecking keys on a variable ratio (VR) 15-min schedule (bottom; from "Within-Session Changes in Responding During Several Simple Schedules," by F. K. McSweeney, J. M. Roll, & J. N. Weatherly, 1994, *Journal of the Experimental Analysis of Behavior*, 62, p. 119; copyright 1994 by the Society for the Experimental Analysis of Behavior, Inc., reprinted with permission). All results are for the mean of all subjects responding during the last 5 of the 30 sessions for which each schedule was available. The results presented at the top were averaged over five delays to postsession feedings.

tization-habituation to suggest that common factors produce both phenomena. In the second part, we show that many alternative explanations for within-session changes in operant responding can be dismissed. In the third part, we consider some of the theoretical and methodological implications of the sensitization-habituation hypothesis. Elaborating these arguments is important because we do not take a position on the theoretical variables that produce sensitization-habituation. Many theories of sensitization-habituation have been proposed (e.g., Sokolov, 1963; Wagner, 1976), but no one theory has gained universal acceptance. For example, the most specific theory, Wagner's model (e.g., Wagner, 1976), has been severely criticized (e.g., Mackintosh, 1987). Even in the absence of a theoretical explanation, however, the sensitization-habituation hypothesis has important theoretical and methodological implications for two large areas of psychological research.

Throughout this article, within-session changes in operant responding are represented by changes in the proportion of total-session responses, rather than by changes in absolute response rates. This is done because the variables that control absolute response rate and those that control the within-session pattern of responding often differ. Figure 2 illustrates this point. It represents the rate of responding (responses per minute, top) and the proportion of total-session responses (bottom) during successive 5-min intervals in the session for subjects maintained at 75%, 85%, or 95% of their free-feeding body weights. The top shows that changing deprivation altered the absolute rate at which subjects responded, as would be expected (e.g., Clark, 1958). The bottom shows that manipulating deprivation did not alter the within-session pattern of responding. Instead, the use of proportions provided a measure of the within-session pattern that was unconfounded by the differences in absolute response rates (see also Figure 4). The use of proportions also facilitates comparison of the operant and sensitization-habituation literatures. Results in the literature on sensitization-habituation are often normalized for differences in absolute response rates.

Empirical Similarities

The exact characteristics of sensitization-habituation may vary from preparation to preparation (e.g., Hinde, 1970). Nevertheless, several fundamental (i.e., frequently reported) characteristics of sensitization-habituation are also shared by within-session changes in operant responding. The characteristics described in this section briefly are that habituation is faster and more pronounced for higher than for lower rates of stimulus presentation, sensitization-habituation cannot be attributed to effector fatigue, habituated responding recovers over time (spontaneous recovery), sensitization-habituation changes with experience, changes in the manner of stimulus presentation can change the rate of habituation, sensitization-habituation is produced by retrospective not by prospective factors, and sensitization-habituation is a relatively general phenomenon. In addition, we show that a single mathematical model provides a good description of results taken from both literatures. Two other frequently reported characteristics of sensitization-habituation, dishabituation and stimulus specificity, have not yet

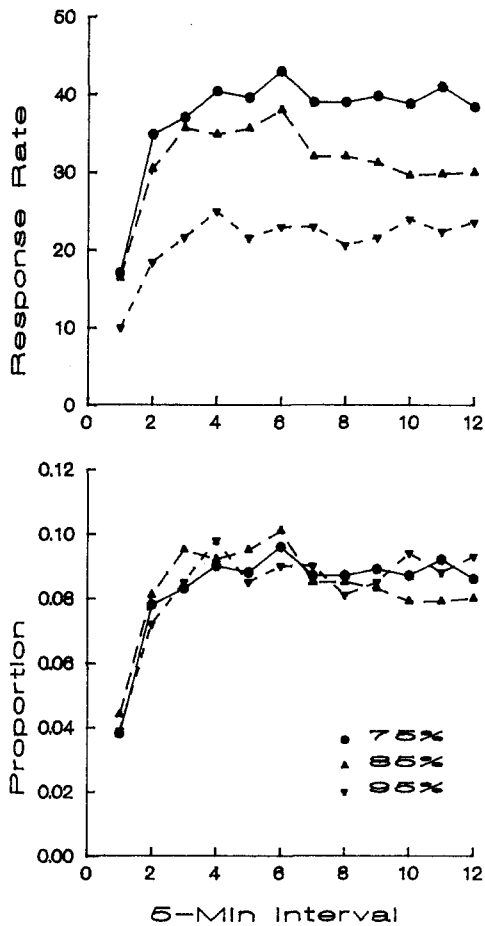


Figure 2. Rate of responding (responses per minute, top) and proportion of total-session responses (bottom) during successive 5-min intervals in the session when subjects were maintained at 75%, 85%, and 95% of their free-feeding body weights. Results were averaged over all subjects responding during the last five sessions for which a condition was conducted (from "Satiety Contributes Little to Within-Session Decreases in Responding," by J. M. Roll, F. K. McSweeney, K. S. Johnson, & J. N. Weatherly, 1995, *Learning and Motivation*, 26, p. 331; copyright 1995 by Academic Press; adapted with permission).

been shown for within-session changes in operant responding. They may be regarded as predictions of the present model.

Rate of Stimulus Presentation

Habituation is often faster and more pronounced (larger) when stimuli are presented at higher rather than lower rates (e.g., Thompson & Spencer, 1966; but also see Hinde, 1970). Likewise, operant responding usually peaks earlier and declines more steeply when reinforcers are presented at higher rather than lower rates (McSweeney, 1992; McSweeney, Roll, & Cannon, 1994; McSweeney, Weatherly, & Swindell, 1995b).

Figure 3, taken from McSweeney (1992), illustrates this point. It represents the proportion of total-session responses during successive 5-min intervals (components) in the session for the mean of all subjects responding on each of five different

multiple schedules. The schedules delivered programmed rates of reinforcement that varied from 15 (multiple VI 240-s VI 240-s) to 240 (multiple VI 15-s VI 15-s) reinforcers per hour in different conditions. Each function represents the results for a different multiple schedule. Figure 3 shows that the peak rate of responding was reached earlier and the decreases in responding were larger for schedules that provided higher rather than lower rates of reinforcement. For example, the peak rate of responding was reached during the second 5-min interval for the multiple VI 15-s schedule but during the sixth 5-min interval for the multiple VI 240-s schedule. The reported proportions varied from .02 to .15 for the multiple VI 15-s VI 15-s schedule but from .07 to .11 for the multiple VI 240-s VI 240-s schedule.

Effector Fatigue Can Be Ruled Out

Sensitization-habituation is not produced by variables related to the act of responding such as muscular warmup or *fatigue* (e.g., Thompson & Spencer, 1966). In fact, many definitions of sensitization-habituation require that effector fatigue be ruled out before these terms can be used (e.g., Thorpe, 1966).

Factors related to the act of responding also contribute little to within-session changes in operant responding (e.g., McSweeney, 1992; McSweeney & Johnson, 1994; McSweeney, Weatherly, & Roll, 1995; McSweeney, Weatherly, Roll, & Swindell, 1995; Melville, Rybiski, & Kamrani, in press; Weatherly, McSweeney, & Swindell, 1995, in press). For example, Weatherly, McSweeney, and Swindell (1995) reduced the rate at which pigeons pecked keys on a VI 1-min schedule by signaling the availability of reinforcers. The within-session pattern of responding did not change even when rate of responding was re-

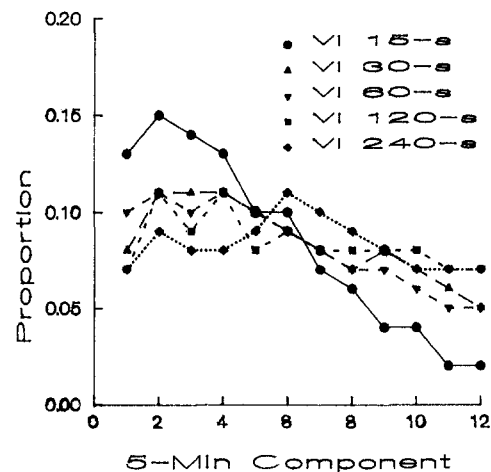


Figure 3. Proportion of total-session responses during successive 5-min intervals (components) for rats pressing levers for Noyes pellets in McSweeney (1992). Subjects responded on five different variable interval (VI) schedules, ranging from VI 15 s to VI 240 s in different conditions. Each function represents the results for the mean of all subjects responding on a particular multiple schedule. All results are from the last 5 of the 30 sessions for which subjects responded on each schedule.

duced from more than 60 responses to less than 10 responses per minute. It seems unlikely that subjects would warmup and fatigue at the same rate when responding at such different rates.

McSweeney, Weatherly, Roll, et al. (1995) studied responding when the response that produced reinforcers changed at 10, 20, 30, or 40 min after the beginning of the 60-min session in different conditions. For example, the effective operandum changed from a lever to a key for rats and from a treadle to a key for pigeons. The within-session patterns of responding during these "switch" conditions did not differ from the patterns during baseline conditions in which subjects performed the same response throughout the session. If muscular warmup produced the early-session increases in responding, then this warmup should have occurred whenever a new operandum was introduced. If fatigue produced the late-session decreases, then subjects should have been more fatigued when they had responded on the same operandum throughout the session than when a new operandum was introduced. To explain these results in terms of response-related factors, we would have to assume complete transfer of warmup and fatigue across responses that use different muscles and occur at different rates. This seems unlikely.

It might be objected that responses, such as key pecking and lever pressing, require so little effort that they do not produce fatigue during operant sessions of ordinary length. In that case, differences in response rate or topography would not produce differences in fatigue and the results reported above could be dismissed. If this argument is accepted, however, effector fatigue is clearly ruled out as an explanation for within-session changes in operant responding. Within-session changes occur for responses such as key pecking and lever pressing during sessions of ordinary length (e.g., Figure 1). If key pecking and lever pressing do not fatigue, then within-session decreases in these responses obviously cannot be attributed to the accumulation of fatigue.

Spontaneous Recovery

Habituated responding usually recovers as time passes since the last stimulus presentation (e.g., Thompson & Spencer, 1966). Figure 4, taken from McSweeney and Johnson (1994), shows that spontaneous recovery also occurs for within-session changes in operant responding. Subjects responded during two successive 50-min sessions. The sessions were separated by 2 to 3, 10, or 30 min spent either inside or outside of the experimental enclosure in different conditions. Figure 4 represents the rate of responding (responses per minute, top) and the proportion of total-session responses (bottom) during successive 5-min intervals in the first (solid line) and second (dashed line) sessions. Results were averaged over all subjects and conditions. Finding similar within-session patterns of responding in the first and second sessions (bottom) indicates that this pattern recovers when an interval of time passes between sessions.

Figure 4 shows that spontaneous recovery occurs for operant responding when spontaneous recovery is defined as a *recovery* of the within-session pattern of responding when time passes between sessions. In contrast, spontaneous recovery, defined as an *increase* in responding from the end of one session to the beginning of the next, is not always observed. In our experience,

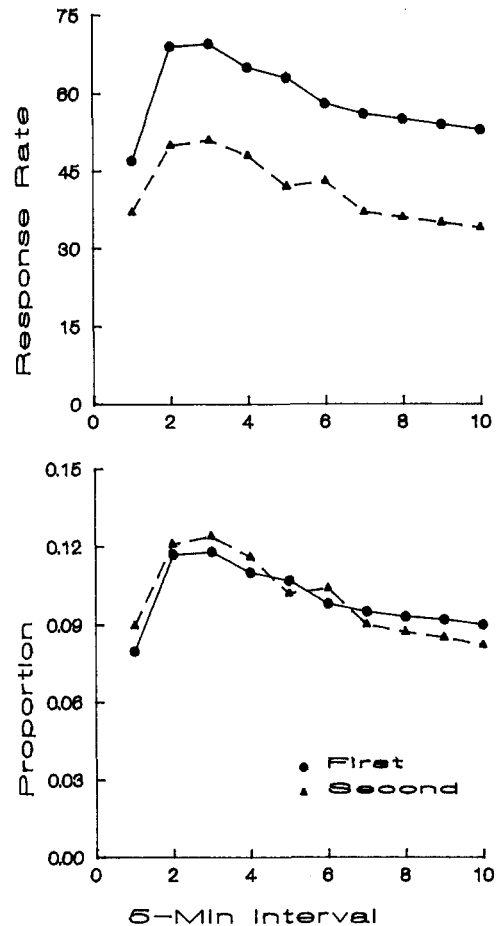


Figure 4. Rate of responding (response per minute, top) and proportion of total-session responses (bottom) during successive 5-min intervals of the first (solid line) and second (dashed line) of two consecutive experimental sessions. Data (from "The Effect of Time Between Sessions on Within-Session Patterns of Responding," by F. K. McSweeney and K. S. Johnson, 1994, *Behavioural Processes*, 31, p. 214; copyright 1994 by Elsevier, Inc.; reprinted with permission) have been averaged over the last five sessions for which all subjects responded during the six experimental conditions.

operant responding increases from the end of one session to the beginning of the next only when the procedure generates a pattern in which responding is faster at the beginning than at the end of the session. For example, schedules that provide high rates of reinforcement (e.g., multiple VI 15-s VI 15 s) usually support a high rate of responding at the beginning of the session that declines steeply as time passes (e.g., McSweeney, 1992; see Figure 3). As a result, responding increases from the end of one session to the beginning of the next. Schedules that provide lower rates of reinforcement support slower responding early in the session, which increases to a peak and then declines somewhat (e.g., McSweeney, 1992; see Figure 3). As a result, responding does not always increase from the end of one session to the beginning of the next.

The course of sensitization-habituation changes with experience. The form taken by sensitization-habituation may

change with experience. This is sometimes interpreted to mean that both short-term (minutes to hours) and long-term (hours to days or weeks) processes contribute (e.g., Carew, 1984; Castellucci & Kandel, 1976; Thompson & Spencer, 1966; Wagner, 1976). The changes in responding that occur within sessions are usually attributed to short-term factors (e.g., Brunner & Maldonado, 1988) because they occur over a few minutes to hours (e.g., Castellucci & Kandel, 1976). Such changes are often considered to be unlearned because they occur during the first session of training. Changes in the pattern of responding between sessions are often attributed to long-term factors (e.g., Brunner & Maldonado, 1988) because they persist over longer periods such as hours, days, or weeks (e.g., Castellucci & Kandel, 1976). Because these changes are altered by experience, they are sometimes considered to be learned (e.g., Wagner, 1976; but also see Macintosh, 1987).

Likewise, within-session changes in operant response rates are present during the first session of training (short-term factors) and experience alters the form of those changes (long-term factors; e.g., McSweeney, 1992; McSweeney et al., 1995b). Figure 5, taken from McSweeney (1992), represents the proportion of total-session responses during successive 5-min intervals (components) in the session for the mean of all subjects responding during Session 1 (solid line) and during Sessions 26–30 (dashed line) of exposure to a multiple VI 1-min VI 1-min schedule. Within-session changes in responding occurred during Session 1 (short-term factors) and further experience with the schedule modified the form of these changes (long-term factors).²

Habituation may become faster and larger over repeated sessions (e.g., Carew, 1984; Groves & Thompson, 1970; Thompson & Spencer, 1966; but also see Brunner & Maldonado, 1988; and Pinsker, Kupfermann, Castellucci, & Kandel, 1970). Sensitization may also decline with experience (e.g., Groves & Thompson, 1970). Both of these changes are apparent in Fig-

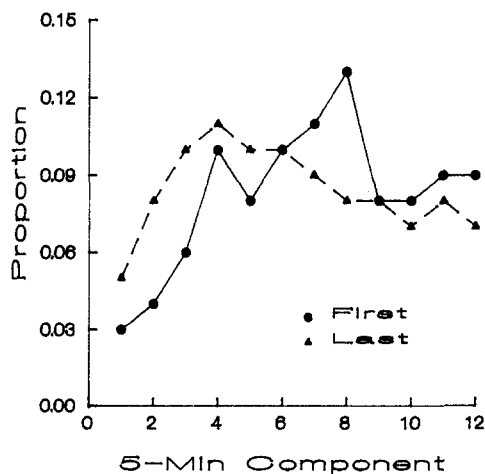


Figure 5. Proportion of total-session responses during successive 5-min intervals (components) during the first recorded session of responding (solid line) and during the last 5 of 30 sessions (dashed line). Results have been averaged over all subjects responding (from McSweeney, 1992, Experiment 2).

ure 5. That is, sensitization was smaller (smaller early-session increases in responding), and habituation was faster (earlier peak rate of responding and larger decreases in responding) in Sessions 26–30 than in Session 1. However, these changes in the within-session pattern of operant responding with experience are not always observed. We have not found a general tendency for the peak rate of responding to occur earlier in the session with experience when we have examined all of our data. Instead, the within-session pattern of responding appears to change from an unconditioned form to whatever form is appropriate for the particular parameters in use in the experiment. For example, the peak occurs earlier with experience if stimuli are presented at a high rate. The peak occurs later with experience if stimuli are presented at a low rate.

Role of stimulus conditions. Sensitization and habituation are altered by changes in the manner of stimulus presentation (e.g., Hinde, 1970). Likewise, the form of the within-session changes in operant response rates is sensitive to the exact experimental conditions. Within-session patterns may differ for subjects responding on multiple and mixed schedules that provide the same programmed rate of reinforcement (Weatherly & McSweeney, 1995). Changing the stimulus that signals the components may also change the within-session pattern when subjects respond on multiple schedules (Weatherly & McSweeney, 1995).

Figure 6 provides an example of this sensitivity to stimulus conditions. The top compares responding for pigeons pecking keys on a fixed interval (FI) 15-s (solid line; McSweeney, Roll, & Weatherly, 1994) and on a VI 15-s schedule (dashed line; McSweeney, Weatherly, & Swindell, 1996). The bottom compares responding when rats press levers on a multiple VI 15-s VI 15-s (solid line; McSweeney, 1992) and on a VI 15-s schedule (dashed line; McSweeney et al., 1996). Both graphs represent the proportion of total-session responses during successive 5-min intervals in the session for the mean of all subjects. The within-session patterns of responding were different for different schedules, and the results are consistent with the literature on sensitization–habituation. As at the top, sensitization–habituation is often faster and more pronounced when stimuli are delivered at fixed rather than at variable intervals of time (e.g., Broster & Rankin, 1994; Davis, 1970; but also see Graham, 1973).³

² The results presented in Figure 4 seem to contradict the idea that within-session patterns of operant responding change with experience. In the figure, the within-session pattern of responding did not differ during the first and second of two consecutively conducted sessions. However, this contradiction is only apparent. Studies reporting that sensitization–habituation changes with experience compare responding during the first session with responding during a small number of following sessions (usually fewer than 5). The results presented in Figure 4 were collected only after subjects had responded on the procedure for many sessions (at least 14). The changes in the within-session patterns of operant responding with experience were probably complete before the data in Figure 4 were collected.

³ Figure 6 can be criticized because it compares results across studies. Therefore, the reported differences in the within-session patterns of responding might be produced by unknown procedural differences between the studies, rather than by differences in the manner of stimulus presentation. However, the procedures used in these studies were similar. For example, all sessions were 60 min long. All experiments con-

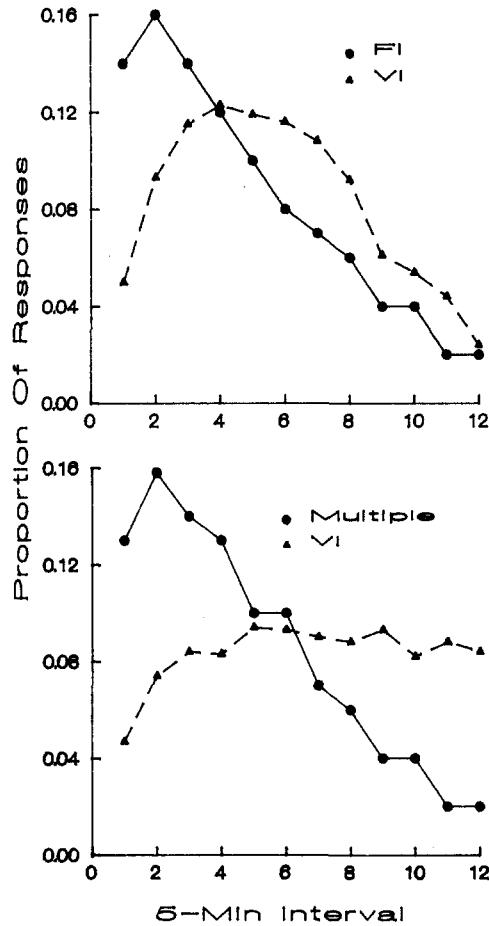


Figure 6. The top axes represent the proportion of total-session key pecks by pigeons responding on fixed interval (FI) 15-s (solid line) and variable interval (VI) 15-s (dashed line) schedules during successive 5-min intervals in the session (results for the FI schedule are from "Within-Session Changes in Responding During Several Simple Schedules," by F. K. McSweeney, J. M. Roll, & J. N. Weatherly, 1994, *Journal of the Experimental Analysis of Behavior*, 62, p. 112; copyright 1994 by the Society for the Experimental Analysis of Behavior, Inc.; adapted with permission; those for VI schedules are from "Within-Session Changes in Responding During Variable Interval Schedules," by F. K. McSweeney, J. N. Weatherly, and S. Swindell, 1996, *Behavioural Processes*, 36, p. 72; copyright 1996 by Elsevier, Inc.; adapted with permission. The bottom axes represent the proportion of total-session lever presses by rats responding on multiple VI 15-s VI 15-s (solid line) and VI 15-s schedules during successive 5-min intervals in the session. The results for multiple schedules are from McSweeney (1992) and those for VI schedules are from McSweeney et al. (1996).

ducted at least five schedules of reinforcement for 30 sessions each. Programmed rate of reinforcement was varied across conditions, and the same five rates were included in all cases. All data were from the last 5 sessions for which subjects responded on a particular schedule. Because the experiments were conducted in the same laboratory, other factors such as the maintenance conditions of the subjects, the postsession feedings, and so forth were also similar. As indicated earlier, the manner of stimulus presentation has also altered within-session patterns of responding within single studies (Weatherly & McSweeney, 1995).

Role of retrospective factors. Several plausible explanations for within-session changes in operant responding attribute them to the anticipation of events that occur in the future (prospective factors). For example, responding might decrease late in the session if the handling that followed the session was aversive and produced a classically conditioned slowing of operant responding (e.g., Estes & Skinner, 1941). Responding might also decrease late in the session if subjects anticipated the feedings that followed the session and if that anticipation produced anticipatory contrast during the session (e.g., Flaherty & Checke, 1982). Evidence that supports these theories would immediately rule out an explanation in terms of sensitization-habituation. Although there are many different theories of sensitization-habituation (e.g., Kandel, Castellucci, Pinsker, & Kupfermann, 1970; Sokolov, 1963; Stein, 1966), all researchers agree that past exposure to a stimulus produces these processes (retrospective factors). We do not know of a theory that attributes sensitization-habituation to the anticipation of events to come (prospective factors).

Prospective explanations for the within-session changes in operant responding can be ruled out. Figure 7, from McSweeney, Weatherly, & Swindell (1995a), represents the rate of responding (responses per minute) during successive 5-min intervals when the session terminated after 20, 40, 60, 80, or 100 min, determined randomly at the beginning of the session. Each function represents results for the mean of all subjects responding during sessions of a particular length. Responding increased and then decreased within sessions, even though subjects could not anticipate when the session would end. These results question reasonable prospective explanations. On the basis of such

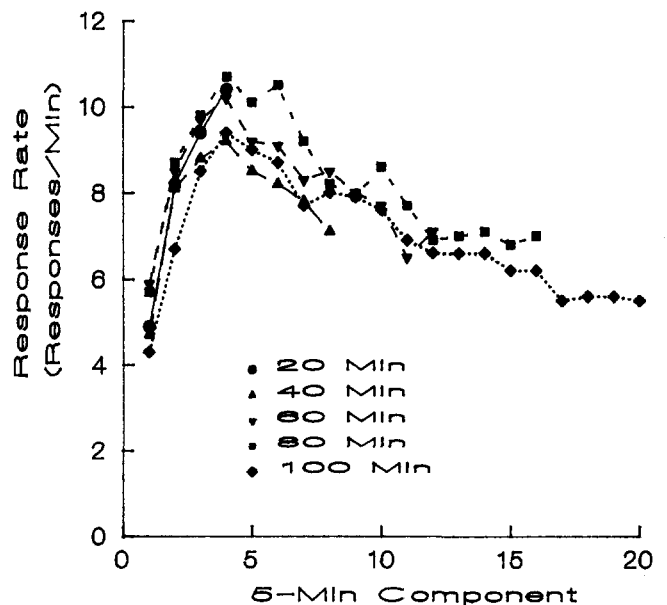


Figure 7. Rate of responding (responses per minute) during successive 5-min intervals in the session when sessions were 20, 40, 60, 80, or 100 min long, determined randomly. Data have been averaged over all subjects and over five experimental sessions (from McSweeney, Weatherly, & Swindell, 1995a). The results for sessions of different lengths are difficult to distinguish.

explanations, within-session changes should not occur if subjects cannot anticipate the events that follow the session. The results are compatible with retrospective explanations. Retrospective factors, which accumulate from the beginning of the session, should occur similarly, regardless of whether subjects can or cannot anticipate the end of the session.

General phenomena. Sensitization-habituation occurs for many different types of stimuli, responses, and species of animals (e.g., Harris, 1943; Pinsky et al., 1970; Thorpe, 1966). Although exceptions exist (e.g., Hinde, 1970), the characteristics of these processes are also similar across species, responses, and stimuli (e.g., Baker & Tiffany, 1985; Pinsky et al., 1970; Thompson & Spencer, 1966).

Within-session changes in operant responding have been reported in many different laboratories when many different procedures are used (see McSweeney & Roll, 1993, for a review). They have been reported for subjects ranging from cockroaches to people. When this question has been explicitly addressed, within-session changes have been found to occur for similar reasons for different responses, reinforcers, and species (e.g., McSweeney, Roll, & Cannon, 1994; McSweeney, Weatherly, & Roll, 1995; McSweeney et al., 1995b).

Quantitative similarities. The bitonic form of many within-session changes in operant response rates (see Figure 1) is similar to the bitonic form of the changes in responding in the literature on sensitization-habituation (e.g., Groves & Thompson, 1970). In both cases, the increases in responding are also observed without the decreases and vice versa (e.g., see Figure 1; and Davis, 1974b). However, arguments about similarity in form would be strengthened if both types of changes in responding could be described by the same quantitative model. Showing that both changes conformed to the same equation would provide a more specific test of their similarity than simply arguing that increases and decreases in responding are observed in both cases.

Operant responding. To develop a quantitative model, we examined the fit of a wide range of potential equations to the within-session changes in operant responding. A quadratic equation was fit to the proportion of total responses over the whole session. Then, a number of other models were constructed on the argument that different equations might describe the early-session increases and the late-session decreases in responding. A series of equations was developed based on all possible additive and multiplicative combinations of the linear, exponential, hyperbolic, and power functions presented in Table 1. These four equations were chosen because they appear to provide the simplest monotonic equations that could describe actual performance. They also provide good descriptions for many behavioral data (e.g., Wixted & Ebbesen, 1991). When the equations in Table 1 were combined, the number of free parameters was reduced to three. An equation based on each reduction was tested if this reduction could be accomplished in more than one way. In Table 1, p is the proportion of total-session responses during a 5-min interval in the session; T is the ordinal number of that 5-min interval within the session; and a , b , and c are free parameters.

The resulting equations were fit to 106 sets of data.⁴ The data included results for rats and pigeons performing several different types of responses (key peck, treadle press, key press, or

Table 1
Equations That Were Fit to Within-Session Changes in Responding

Function	Equation
Linear	$p = aT + b$
Exponential	$p = b/(e^{aT})$
Power	$p = aT^b$
Hyperbolic	$p = [aT/(a + T)]/T$
Quadratic	$p = aT^2 + bT + c$

Note. p is the proportion of the total-session responses emitted during a 5-min interval; T is the ordinal number of the 5-min interval within the session; a , b , and c are free parameters.

lever press) for food (mixed grain, Noyes pellets, or sweetened condensed milk) and water reinforcers delivered by several different procedures (VR, FI, differential reinforcement of low rates of responding [DRL], multiple VI VI, concurrent VI VI, and delayed matching to sample). All equations were fit to the data using the nonlinear estimation procedure in SYSTAT (Wilkinson, 1990). This program uses an iterative procedure to yield the best least-squares fit. The two available minimization methods, quasi-Newton and simplex, produced identical results. The maximum iterations used to fit the data was usually 20. In a few cases, the number of iterations was extended to 40 because of variability in the data.

Only 4 of the tested equations often accounted for more than 80% of the variance in the data. The successful equations were the difference between a hyperbolic and an exponential equation, between a hyperbolic and a linear equation, between a linear and a hyperbolic equation, and an exponential times a linear equation. The difference between a hyperbolic (increases in responding) and an exponential (decreases in responding) equation provided the best overall fit (largest r^2) among these models. This model appears in Equation 1.

$$p = \frac{b}{e^{aT}} - \frac{c \times T}{c + T} \times \frac{1}{T} \quad (1)$$

As in Table 1, p is the predicted proportion of the total-session responses that should occur during successive 5-min intervals in the experimental session (T); a , b and c are free parameters; a and b govern habituation, and c applies to sensitization.

Figure 8 represents frequency distributions of the sizes of the a , b , and c parameters and the proportion of the variance in the data accounted for by Equation 1. Results for a few sets of data were not reported in Figure 8 because their parameters were outliers. Therefore, the total reported frequencies may differ from 106.

Equation 1 is parsimonious. At least two free parameters are needed to describe bitonic within-session changes in responding. Equation 1 describes the changes with only three param-

⁴ The sources of the data were McSweeney (1992); McSweeney et al. (1990); McSweeney, Roll, and Cannon (1994); McSweeney, Roll, and Weatherly (1994); McSweeney, Weatherly, and Roll (1995); and McSweeney, Weatherly, and Swindell (1995a), (1995b), (1996), and (in press).

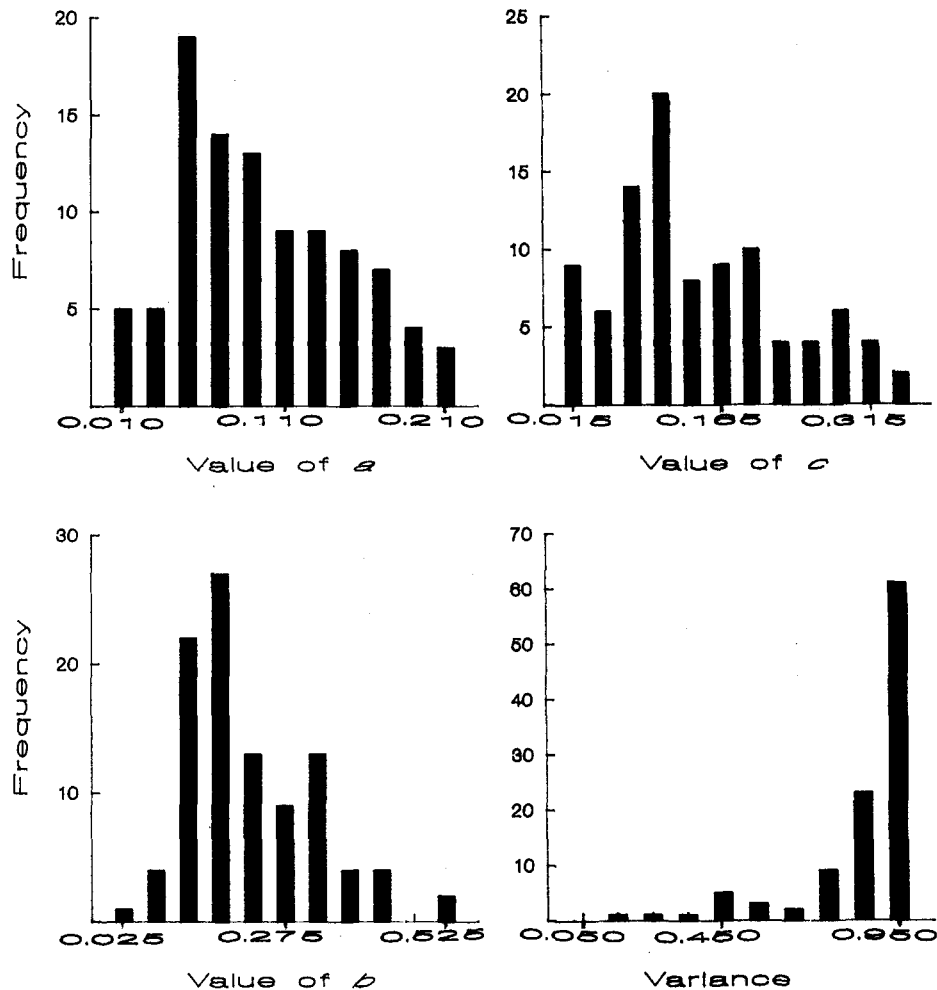


Figure 8. Frequency distributions of the size of the a (top left), b (bottom left), and c (top right) parameters and the proportion of the variance in the data accounted for (bottom right) when Equation 1 was applied to within-session changes in operant responding.

ters. Equation 1 also describes many data well. Figure 8 shows that it accounted for a median proportion of the variance in the data of .92. The worst fits occurred when the data were noisy (e.g., for pigeons; McSweeney, Roll, & Cannon, 1994) or when responding changed little within the session. For example, when programmed rate of reinforcement varied within an experiment, the median r^2 was higher for the two schedules that provided the highest rates of reinforcement (median = .97) than for the two schedules that provided the lowest rates (median = .81). This occurred because the within-session changes in responding became flatter as the rate of reinforcement decreased (see Figure 3). When substantial within-session changes occurred (high rates of reinforcement), the equations fit the data well.

Sensitization-habituation. Equation 1 also provides a good description of results taken from the sensitization-habituation literature. We searched this literature for studies whose researchers examined the behavior of animals that had not been subjected to intrusive physiological or drug manipulations. We looked for

studies whose researchers examined the behavior of a wide variety of species, performing a variety of responses, to a variety of stimuli. These included both laboratory and field studies. Data were included only if responding changed when a stimulus was presented repeatedly or for a prolonged period. This was necessary because field studies often had several behaviors recorded, only some of which changed with the experimental manipulation. To be included, a dataset had to contain at least eight points, which provided a serious test of an equation containing three parameters. Altogether we obtained 145 datasets.⁵

We read all results from graphs, so they may be slightly inaccurate. We converted them to proportions of total responding so that Equation 1 could be fit. We used time and number of

⁵ The sources of the data were Barrass (1961; male spider sexual response to an unresponsive female); Brunner and Maldonado (1988; crab withdrawal from a shadow stimulus); Cook (1971; snail responsiveness to light off, vibration, or both); Davis (1970, 1974a, 1974b; rat startle response); Davis and Gendelman (1977; rat startle response);

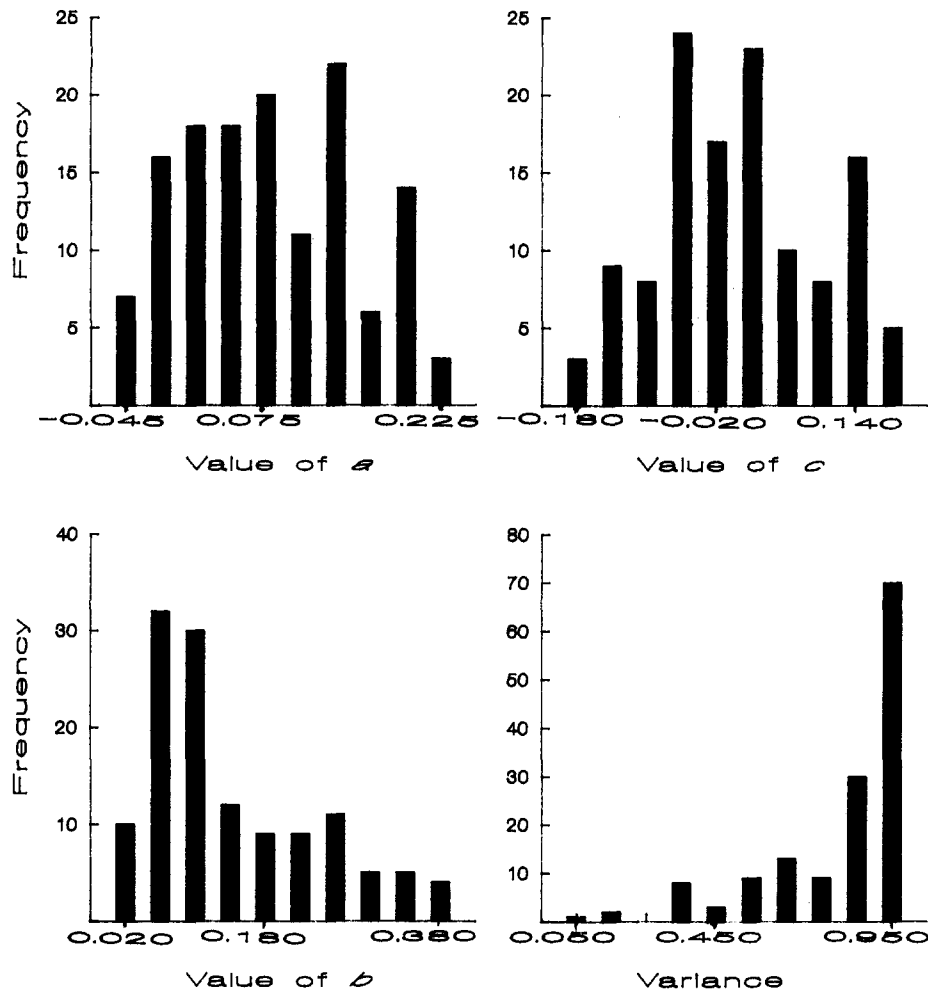


Figure 9. Frequency distributions of the size of the a (top left), b (bottom left), and c (top right) parameters and the proportion of the variance in the data accounted for (bottom right) when Equation 1 was applied to the behavioral measures of intact organisms in the sensitization-habituation literature.

stimulus presentations interchangeably as the independent variable because changes in responding to repeated and prolonged stimuli are both considered to be examples of sensitization-habituation (e.g., Hinde, 1970). Time and number of stimuli may

also be used interchangeably in quantitative models of habituation. For example, Petrinovich (1984) argued that time bins of any size may be used in place of number of trials as the independent variable in quantitative models.

Figure 9 represents frequency distributions of the sizes of the a , b , and c parameters, as well as of the proportion of the variance accounted for, when Equation 1 was fit to studies from the sensitization-habituation literature. Figure 9 shows that Equation 1 describes the data well, accounting for a median proportion of variance in the data of .89. The a , b , and c parameters were somewhat smaller for sensitization-habituation than they were for operant responding. The median sizes of a , b , and c were .090, .196, and .124, respectively, for operant responding and .082, .111, and .017, respectively, for sensitization-habituation.

Eisenstein and Peretz (1973; contraction of protozoa to a mechanical stimulus); Epstein, Rodefer, Wisniewski, and Caggiula (1992; human responsiveness to a taste); Goodman and Weinberger (1973; responsiveness of toads to intruding prey and of mudpuppy salamanders to a shadow); Kimble and Ray (1965; frog wiping reflex); Kling and Stevenson (1970; male chaffinch chink response to a stuffed owl); Patterson and Petrinovich (1979; white-crowned sparrows responsiveness to song); Peeke, Avis, and Peeke (1979; convict cichlid aggressive responses to an intruder); Petrinovich and Patterson (1979; white-crowned sparrow responsiveness to song); Petrinovich and Peeke (1973; white-crowned sparrows responsiveness to song); Pinsker et al. (1970; *Aplysia* gill withdrawal to a tactile stimulus); Rankin and Broster (1992; responsiveness of nematodes to a tap); Swithers and Hall (1994; rat oral responsiveness); Swithers-Mulvey and Hall (1992, 1993; rat oral responsiveness); Swithers-Mulvey et al. (1991; rat oral

responsiveness); Swithers-Mulvey, Mishu, and Hall (1992; rat oral responsiveness); and Williams, Hamilton, and Carlton (1974; 1975; rat startle response).

Figures 8 and 9 show that the same equation can provide a good description of the results from the operant and sensitization–habituation literatures when data are analyzed in a similar way and when the results for sensitization–habituation are restricted to behavioral measures taken from physiologically intact organisms. This indicates that the quantitative form of the temporal changes in responding is similar for the two types of behavior. Because only four equations provided even an adequate description of the operant data, finding these quantitative similarities provides a relatively specific test of the similarities in the temporal pattern of responding in the two literatures. It goes far beyond the simple statement that responding usually increases and then decreases in both cases.

Untested Characteristics

Two frequently reported characteristics of sensitization–habituation have not yet been studied for within-session changes in operant responding. First, responding to a habituated stimulus is often restored after a novel stimulus is presented. That is, dishabituation occurs (e.g., Thompson & Spencer, 1966). Second, responding increases if a novel stimulus is substituted for the habituated stimulus (e.g., Swithers & Hall, 1994). That is, habituation is relatively specific to the stimulus presented (stimulus specificity). Therefore, finding these characteristics may be regarded as predictions of the present model.

Alternative Explanations

Sensitization–habituation is relatively unique in its ability to describe within-session changes in operant responding because many alternative explanations for these changes can be dismissed. We have already discussed several inadequate explanations. For example, within-session changes cannot be attributed to muscular warmup or fatigue (see *Effector Fatigue Can Be Ruled Out*). They cannot be attributed to anticipation of factors that follow the session, such as the postsession feedings or handlings (see *Role of retrospective factors*). Several other explanations can similarly be dismissed.

The early-session increases in responding are not produced by recovery from handling. Responding increased early in the second of two consecutive sessions, regardless of whether subjects spent the time between sessions inside or outside of the experimental enclosure (McSweeney & Johnson, 1994). That is, the early-session increases in responding were observed in the second session, regardless of whether subjects were or were not handled before that session.

Changes in attention to the experimental task probably do not explain within-session changes in operant responding. The concept of *attention* has many possible operational definitions. To date, two of these definitions have been tested. First, changes in the accuracy of responding during delayed-matching-to-sample (DMTS) procedures are often taken as an index of changes in attention to the task (e.g., McCarthy & Voss, 1995). However, McSweeney et al. (in press) reported that the accuracy of responding (percentage correct) during a DMTS procedure did not change within sessions, even though the rate of responding on the sample stimulus did change. Second, responding might be more closely controlled by the operant contingency when

subjects attend to the instrumental task. However, McSweeney, Roll, and Weatherly (1994) found that responding decreased within sessions, regardless of whether subjects responded on VR, FI, or DRL procedures. If sensitivity to the operant contingency changed systematically within sessions, then subjects should have responded faster on VR schedules (fast responding is reinforced) at times when they responded more slowly on DRL schedules (slow responding is reinforced). This did not occur (see also McSweeney, Weatherly, & Swindell, in press).

Changes in arousal probably do not produce within-session changes in responding. Arousal is usually considered to be a state of the animal that determines the “energy” level of its behavior (e.g., Duffy, 1962). McSweeney, Swindell, and Weatherly (in press-a) studied rats pressing levers for food reinforcers. A drinking spout or running wheel was also available during some conditions but not during others. The correlation between the rate of lever pressing and the rate of drinking or running at a particular time in the session was inconsistently positive or negative. It was not consistently positive as it should have been if changes in all of these behaviors were produced by changes in a single state of arousal. These results cannot be reconciled with changes in arousal without attributing the changes in instrumental responding to one type of arousal and the changes in adjunctive licking or running to a second type of arousal. Unfortunately, the concept of *arousal* would lose its predictive value if additional states were postulated to describe changes in each type of behavior.

Changes in one type of interfering behavior, adjunctive behaviors, do not produce the within-session changes in instrumental responding. In the study above, the drinking spout and running wheel were positioned so that responding on them would interfere with instrumental lever pressing. Within-session changes in the frequency of these interfering responses did not produce the within-session pattern of instrumental responding. First, the within-session pattern of instrumental responding was not different when adjunctive licking or running was allowed and when it was not. Second, the correlation between the rate of pressing and the rate of licking or running at a particular time in the session was not consistently negative, as it should have been if one type of behavior interfered with the other.

Satiation for the reinforcer can also be questioned as an explanation for the late-session decreases in responding. To clarify the difference between satiation *for* the reinforcer and sensitization–habituation *to* the reinforcer, *satiation* usually refers to all of the factors that control the consumption of ingestive stimuli, such as food and water. Sensitization–habituation to the sensory qualities of these stimuli may contribute to this satiation, but additional factors such as gastric load, postingestive consequences, and the nutritional state of the organism also contribute.

We prefer sensitization–habituation to satiation as an explanation for within-session changes in operant responding for three reasons. First, manipulation of several variables, which are traditionally thought to contribute to satiation, produces little or no effect on the within-session pattern of operant responding. For example, in three experiments, Roll, McSweeney, Johnson, and Weatherly (1995) varied the caloric density of the reinforcer, the size of the reinforcer, and the subjects’ depriva-

tion, either by feeding them before the session or by varying the percentage of their free-feeding body weights at which they responded (75% to 95%). Prefeeding the subjects, varying their percentage of body weight, and changing the caloric density of the reinforcer had no effect on within-session patterns of responding (e.g., bottom of Figure 2). Varying reinforcer size altered within-session patterns, but only when the size of the reinforcer increased by a factor of 5, not by a factor of 3 (see Cannon & McSweeney, 1995, for similar results). In each experiment, the rate of responding averaged over the session changed appropriately with the experimental manipulation (e.g., top of Figure 2). Therefore, it is unlikely that the experimental manipulations did not alter the subjects' level of satiation. In contrast to satiation, these results are consistent with sensitization-habituation. For example, Swithers-Mulvey, Miller, and Hall (1991) showed that changes in deprivation did not alter the pattern of sensitization-habituation to oral infusions of a food as long as the subjects were at least 18 days old when tested.

Second, sensitization-habituation provides a more natural description than satiation of some of the results presented earlier. For example, a relatively complicated and dynamic model of satiation would be required to explain why within-session patterns of responding differed markedly for VI and FI, or for VI and multiple VI VI schedules, that provided comparable rates of reinforcement (see Figure 6). In contrast, such differences are expected if within-session changes are produced by sensitization-habituation.

Third, sensitization-habituation can occur for noningestive (e.g., discriminative stimuli and the experimental context), as well as for ingestive stimuli (e.g., food or water). Satiation is usually restricted to ingestive stimuli. This distinction is important because within-session changes have been observed even when no reinforcers (ingestive stimuli) are presented. For example, within-session changes in lever pressing have been observed before conditioning begins (e.g., Schoenfeld, Antonitis, & Bersh, 1950) and, as discussed later, during extinction (spontaneous recovery).

Before closing this section, we should clarify two points. First, we do not argue that these alternative explanations can never contribute to within-session changes in operant responding. Variables such as fatigue or satiation may contribute if the operant response is very difficult or if the reinforcers are very large. However, we argue that these alternative variables contribute little to the within-session patterns of responding under the relatively standard operant procedures used in many experiments. Under relatively standard conditions, most of the within-session changes in operant responding are produced by sensitization-habituation.

Second, we do not argue that rejection of these alternative explanations shows that sensitization-habituation must produce the within-session changes in operant responding. Instead, we show that sensitization-habituation is not one among many viable hypotheses. It is relatively unique in its ability to describe the currently known characteristics of within-session changes in operant responding.

Implications

The relation between habituation and conditioning has been disputed for years, although researchers have usually compared

habituation with classical, rather than operant, conditioning. For example, it has been argued that habituation is produced by classical conditioning (e.g., Stein, 1966) or that both habituation and classical conditioning are produced by more primitive processes (e.g., Wagner, 1976).

This article takes a different approach. We argue that the empirical phenomena of sensitization and habituation can occur during operant conditioning procedures. That is, because some stimuli, such as the experimental enclosure, are present for a long time and other stimuli, such as reinforcers, are presented repeatedly, sensitization-habituation may occur to those stimuli. This sensitization-habituation may alter the rate of instrumental responding.

The idea that sensitization-habituation may occur during conditioning seems obvious, and it is interesting to ask why this idea was not investigated earlier. Part of the answer may lie in the frequent assumption that sensitization-habituation occurs only to "neutral," not to "biologically important," stimuli, such as reinforcers or unconditioned stimuli. For example, Thorpe's (1966) definition described *habituation* as "the relatively persistent waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement" (p. 74). Some researchers have taken these prescriptions quite seriously. For example, Williams, Hamilton, and Carlton (1974) wrote "stimuli that are demonstrably significant in determining species survival (e.g., food, water and a sexually receptive partner) are immune to habituation" (p. 724). As a result, sensitization-habituation would not be expected during conditioning procedures.

Implications for Operant Conditioning

Determinants of operant responding. If within-session changes in operant responding are produced by the same variables that produce sensitization-habituation, then sensitization-habituation should be added to the list of nonoperant factors that may influence operant responding. For example, Brown and Jenkins (1968) showed that a frequently studied operant response, the key peck, could also be classically conditioned. As a result, the responding observed in operant situations may be produced by both operant and Pavlovian factors (e.g., Gamzu & Schwartz, 1973; Hearst & Jenkins, 1974; Rachlin, 1973). Operant responding may also be altered by adjunctive behaviors (e.g., Falk, 1971; Staddon & Simmelhag, 1971). Altogether, responding in operant situations may be a joint product of factors produced by the response-reinforcer relation (operant responding), the stimulus-reinforcer relation (Pavlovian responding), the spacing of reinforcers in time (adjunctive behaviors), and the repeated or prolonged presentation of stimuli (sensitization-habituation).

Extinction. Sensitization-habituation is compatible with several of the characteristics of extinguished behavior. Both habituated and extinguished responding may be restored by the presentation of a novel stimulus (dishabituation or disinhibition; e.g., Thompson & Spencer, 1966). The recovery of habituated or extinguished responding that occurs with the passage of time may also be smaller when stimulus repetition continues even after responding ceases (habituation or extinction below zero; e.g., Thompson & Spencer, 1966).

Sensitization–habituation may also help to explain the spontaneous recovery of extinguished responding (e.g., Humphrey, 1930; Thompson & Spencer, 1966; Windsor, 1930; but also see Kling & Stevenson, 1970; and Razran, 1956). *Spontaneous recovery* refers to the return of an extinguished response at the beginning of the next session. Most theories of extinction have difficulty explaining this phenomenon without adding special assumptions. For example, Pavlov (1927) argued that responding recovers because inhibition dissipates between sessions. In contrast, sensitization–habituation provides an easy explanation. It could be argued that conditioning establishes the experimental context as a discriminative stimulus for instrumental responding. Responding decreases within sessions of extinction because habituation occurs to this context or to the stimulus properties of the response itself. Responding recovers between sessions of extinction because habituated responding spontaneously recovers.

Positive reinforcers versus aversive stimuli The sensitization–habituation hypothesis may help to explain why within-session changes in operant responding differ when positive reinforcers and aversive stimuli are used. Warmup, the early-session increase in responding, is frequently reported when subjects respond on negative reinforcement (e.g., Dinsmoor, 1962) or punishment procedures (e.g., Azrin, 1956). In contrast, late-session decreases in responding are rarely reported.

Although there are exceptions, sensitization occurs (e.g., Thompson, Groves, Teyler, & Roemer, 1973), but habituation often does not occur when strong stimuli are used (e.g., Groves & Thompson, 1970). Protective reflexes may also not habituate (Kimmel, 1973). Therefore, the early-session increases in responding (warmup) should occur when aversive stimuli are used if these increases are produced by sensitization. The late-session decreases might not occur if they are produced by habituation. In support of this argument, decreasing responding (habituation) was reported during an escape procedure that used a relatively mild aversive stimulus (a light; Jerome, Moody, Connor, & Ryan, 1958).

Operant procedures as baselines. Many experimenters use operant procedures as a baseline for assessing the effect of other manipulations (e.g., physiological or pharmacological interventions). Within-session changes in response rates should be reduced or eliminated to provide steady baselines for these studies. The literature on sensitization–habituation suggests how this could be achieved. Operant responding should be relatively constant if sensitization–habituation is reduced or if it is complete before data are collected. To give only one example, providing a low rate of reinforcement should reduce the amount of sensitization–habituation that occurs to the reinforcers.

Implications for Sensitization–Habituation

Generality. Within-session changes in operant responding suggest that sensitization–habituation is present during steady-state behavior as well as early in training. They also suggest that sensitization–habituation occurs for ingestive (e.g., food), as well as for noningestive (e.g., light), stimuli. Finding sensitization–habituation during operant procedures may eventually prove to be an important extension of its generality. Operant

procedures are often used in applied settings. Therefore, the effectiveness of these applications might be improved if the occurrence of sensitization–habituation could be prevented or used.

A novel perspective on sensitization–habituation. The earlier discussion described two differences between the characteristics of sensitization–habituation and within-session changes in operant responding. First, habituation is often faster in repeated sessions (e.g., Carew, 1984; Groves & Thompson, 1970), but the peak rate of operant responding is not always reached earlier over repeated sessions. Second, responding often increases from the end of one session of sensitization–habituation to the beginning of the next. In contrast, spontaneous recovery is reliably observed for instrumental responding only if it is defined as recovery of the within-session pattern of operant responding with time between sessions (e.g., Figure 4), not when it is defined as an increase in operant responding with time between sessions.

These differences may indicate that there are differences between sensitization–habituation to relatively neutral stimuli and to ingestive stimuli, such as reinforcers. This would not be surprising because the characteristics of sensitization–habituation vary somewhat from one preparation to the next (e.g., Hinde, 1970). Alternatively, the operant data may suggest that the results for sensitization–habituation have been misinterpreted. *Spontaneous recovery* (defined as an increase in responding between sessions) is not always observed in the sensitization–habituation literature (e.g., Davis, 1972; Patterson & Petrinovich, 1979; Petrinovich & Patterson, 1979). Likewise, habituation does not always become faster with experience (e.g., Brunner & Maldonado, 1988; Pinsker et al., 1970). The operant results may help to explain why the literature on sensitization–habituation contains these conflicting data.

As argued earlier, operant responding increases from the end of one session to the beginning of the next only when responding primarily decreases within sessions. Not finding spontaneous recovery for habituated responding may have occurred because the rate of stimulus presentation was not high enough to produce a largely decreasing pattern of responding within the session for the particular preparation under study.

As argued earlier, suppose also that experience changes an unconditioned pattern of operant responding to a pattern that is appropriate for the particular conditions of stimulus presentation used in the study. In that case, responding would peak earlier with experience only if those stimulus conditions supported a within-session pattern of responding that peaked earlier than the unconditioned pattern (e.g., high rate of stimulus presentation). Responding would peak later with experience if the conditions produced a within-session pattern of responding that peaked later than the unconditioned pattern (e.g., low rate of stimulus presentation).

Although it is beyond the scope of this article, these ideas differ from the explanations for these phenomena that usually appear in the sensitization–habituation literature (e.g., Wagner, 1976). Therefore, the predictions of the present model should be tested. To give one example, within a single preparation, experience should produce an earlier peak rate of responding when stimuli are presented at higher, but not lower, rates.

Habituation versus satiation. As argued earlier, decreases in the consumption of ingestive stimuli, such as food or water, that

occur with exposure to those stimuli (satiety) have traditionally been distinguished from the decreases in responding to non-ingestive stimuli that occur with exposure to those stimuli (habituation). Arguing that habituation occurs for reinforcers raises questions about how much of the decreases in responding that are attributed to satiety are actually habituation to the stimulus properties of the ingested stimulus.

This idea is not new (e.g., Dethier, 1976) and some experiments suggest that sensitization-habituation may play a more prominent role in producing satiety than previously suspected (e.g., Swithers & Hall, 1994). In a series of experiments, Swithers, Hall, and their colleagues gave rat pups brief intraoral infusions of food (usually a sucrose solution). Responsiveness to the food, measured by mouthing, increased and then decreased with repeated infusions. The pups also showed "satiety" after several infusions. That is, they ingested less of the food when given the opportunity to consume it freely (Swithers-Mulvey & Hall, 1992). This satiety was produced by changes in oral factors because postingestive consequences were minimized. The rat pups were too young to metabolize sucrose and only small amounts of fluid were delivered, reducing gastric fill. Swithers and Hall (1994) further showed that sensitization-habituation produced the changes in oral responsiveness. Using the same strategy used here, they showed that the changes in responsiveness to the food shared many of the empirical properties of sensitization-habituation to noningestive stimuli. As a result, Swithers, Hall, and colleagues concluded that oral habituation may be the common mechanism through which the many variables associated with satiety (e.g., hydrational state, nutritional state, gastric fill, and blood glucose levels) exert their effect on feeding (Swithers-Mulvey & Hall, 1993). Such an idea is promising and requires additional investigation.

Rate versus temporal patterning of responding. Results, such as those presented in Figures 2 and 4, suggest that different variables control the temporal patterning and the rate of operant responding. Finding that a simple equation, such as Equation 1, provides a good description of results in the operant and sensitization-habituation literatures suggests that the factors that control the temporal patterning of responding are often relatively simple. Only two processes, one described by an exponential decay and the other described by an ascending hyperbolic function, were required to account for approximately 90% of the variance in the data.

Future research might reveal that these two processes also describe the temporal patterning of behavior in other situations. Some evidence suggests that similar within-session changes occur during classical conditioning (e.g., Bruner, 1965; Lubow, 1965; Lyon & Ozolins, 1970; McSweeney, Swindell, & Weatherly, in press-b; Rubin & Brown, 1969; Siegel & Domjan, 1971; Tomie, 1976). Sensitization-habituation has also been suggested as the explanation for some temporal changes in human performance (e.g., changes in vigilance; Mackworth, 1968), as well as for changes in exploration (e.g., Poucet, Durup, & Thinus-Blanc, 1988; Thompson & Spencer, 1966; but also see Williams et al., 1974; and Williams, Hamilton, & Carlton, 1975). Finally, temporal patterns of responding that resemble those reported here have been observed for consummatory responding (e.g., drinking; Rachlin & Krasnoff, 1983), spontaneously occurring behaviors (e.g., activity, locomotion, and exploration;

e.g., Montgomery, 1953a, 1953b), and responses used in conditioning procedures before conditioning begins (e.g., Schoenfeld et al., 1950). If further research confirmed that similar processes governed responding in all of these situations, then a relatively simple and truly general description of the temporal patterning of responding would be provided.

Conclusion

Within-session changes in operant responding share enough of the empirical characteristics of sensitization-habituation to suggest that the two types of changes in responding are produced by similar variables. In both cases, the peak rate of responding is often reached earlier in the session and the decline in responding is steeper when stimuli are presented at higher rather than lower rates. Both changes in responding spontaneously recover over time. Both changes are altered by experience. In both cases, the form of the changes in responding depends on the exact nature of the stimulus conditions. Both phenomena are produced by retrospective factors that accumulate over time, rather than by anticipation of events to come. Neither change can be attributed to effector fatigue. Both are general phenomena that occur for a wide variety of species, performing a wide variety of responses. Finally, the basic form of the changes in responding are similar. The changes are often biconic, but the increases in responding may occur without the decreases and vice versa. When the data from the two literatures are presented in a similar manner, both changes can be described by the difference between a negative exponential decay function (habituation) and an ascending rectangular hyperbola (sensitization).

In addition to describing past results, the sensitization-habituation model suggests directions for future research. As argued earlier (see *Untested Characteristics*), dishabituation and stimulus specificity should be shown for operant responding. In addition, many less frequently reported characteristics of sensitization-habituation should be studied. To give two examples, recovery from habituation has been shown to be faster after faster stimulus presentations than it is after slower stimulus presentations (e.g., Davis, 1970). The spontaneous recovery of a habituated response may also be smaller when the stimulus is presented even after response to it ceases (habituation below zero; e.g., Thompson & Spencer, 1966). Although these characteristics have not been shown often enough to be considered fundamental characteristics of sensitization-habituation, finding any of them for within-session changes in operant responding would add to the substantial weight of evidence in favor of the sensitization-habituation model.

The nature of the stimuli to which animals show sensitization-habituation during operant conditioning also remains to be established. The fact that the presence of discriminative stimuli may alter within-session changes in responding (see Figure 6) indicates that sensitization-habituation may occur to these stimuli. The fact that the rate (see Figure 3) and manner (i.e., FI or VI; see Figure 6) of reinforcer presentation alter the within-session patterns suggests that some sensitization-habituation occurs to the reinforcers. The contribution of other stimuli remains to be established.

The aspect(s) of the reinforcers to which habituation occurs

is also unknown. The similarity of the present within-session changes in operant responding to results reported for sensitization-habituation to the oral properties of food (e.g., Swithers & Hall, 1994) suggests that some habituation occurs to oral aspects of reinforcers (e.g., taste). However, subjects may also habituate to other variables, such as the sound of the feeder or the length of feeder presentation.

Future experiments might also determine whether variables such as fatigue or satiation contribute to within-session changes in operant responding under extreme conditions. The experiments that ruled out these explanations for within-session changes in operant responding used relatively standard operant procedures (e.g., easy to manipulate operanda and intermediate rates of reinforcement). Future experiments should determine whether variables such as fatigue or satiation can supplement the basic sensitization-habituation processes under more extreme conditions (e.g., Cannon & McSweeney, 1995).

References

- Azrin, N. H. (1956). Some effects of two intermittent schedules of immediate and non-immediate punishment. *Journal of Psychology*, *42*, 3-21.
- Baker, T. B., & Tiffany, S. T. (1985). Morphine tolerance as habituation. *Psychological Review*, *92*, 78-108.
- Barrass, R. (1961). A quantitative study of the behaviour of the male *Mormoniella vitripennis* (walker) (*Hymenoptera pteromalidae*) towards two constant stimulus-situations. *Behaviour*, *18*, 288-312.
- Broster, B. S., & Rankin, C. H. (1994). Effects of changing interstimulus interval during habituation in *Caenorhabditis elegans*. *Behavioral Neuroscience*, *108*, 1019-1029.
- Brown, P. L., & Jenkins, H. M. (1968). Auto-shaping of the pigeon's key-peck. *Journal of the Experimental Analysis of Behavior*, *11*, 1-8.
- Bruner, A. (1965). UCS properties in classical conditioning of the albino rabbit's nictitating membrane response. *Journal of Experimental Psychology*, *69*, 186-192.
- Brunner, D., & Maldonado, H. (1988). Habituation in the crab *Chasmagnathus granulatus*: Effect of morphine and naloxone. *Journal of Comparative Physiology*, *162*, 687-694.
- Cannon, C. B., & McSweeney, F. K. (1995). Within-session changes in responding when rate and duration of reinforcement vary. *Behavioural Processes*, *34*, 285-292.
- Carew, T. J. (1984). An introduction to cellular approaches used in the analysis of habituation and sensitization in *Aplysia*. In H. V. S. Peeke & L. Petrinovich (Eds.), *Habituation, sensitization and behavior* (pp. 205-249). New York: Academic Press.
- Castellucci, V., & Kandel, E. R. (1976). An invertebrate system for the cellular study of habituation and sensitization. In T. J. Tighe & R. N. Leaton (Eds.), *Habituation: Perspectives from child development, animal behavior and neurophysiology* (pp. 1-47). New York: Wiley.
- Clark, F. C. (1958). The effect of deprivation and frequency of reinforcement on variable-interval responding. *Journal of the Experimental Analysis of Behavior*, *1*, 221-228.
- Cook, A. (1971). Habituation in a freshwater snail (*Limnaea stagnalis*). *Animal Behaviour*, *19*, 463-474.
- Davis, M. (1970). Effects of interstimulus interval length and variability on startle-response habituation in the rat. *Journal of Comparative and Physiological Psychology*, *72*, 177-192.
- Davis, M. (1972). Differential retention of sensitization and habituation of the startle response in the rat. *Journal of Comparative and Physiological Psychology*, *78*, 260-267.
- Davis, M. (1974a). Sensitization of the rat startle response by noise. *Journal of Comparative and Physiological Psychology*, *87*, 571-581.
- Davis, M. (1974b). Signal-to-noise ratio as a predictor of startle amplitude and habituation in the rat. *Journal of Comparative and Physiological Psychology*, *86*, 812-825.
- Davis, M., & Gendelman, P. M. (1977). Plasticity of the acoustic startle response in the acutely decerebrate rat. *Journal of Comparative and Physiological Psychology*, *91*, 549-563.
- Dethier, V. G. (1976). *The hungry fly: A physiological study of the behavior associated with feeding*. Cambridge, MA: Harvard University Press.
- Dinsmoor, J. A. (1962). Variable-interval escape from stimuli accompanied by shocks. *Journal of the Experimental Analysis of Behavior*, *5*, 41-47.
- Duffy, E. (1962). *Activation and behavior*. New York: Wiley.
- Eisenstein, E. M., & Peretz, B. (1973). Comparative aspects of habituation in invertebrates. In H. V. S. Peeke & M. J. Herz (Eds.), *Habituation. Vol. 2: Physiological substrates* (pp. 1-31). New York: Academic Press.
- Epstein, L. H., Rodefer, J. S., Wisniewski, L., & Caggiula, A. R. (1992). Habituation and dishabituation of human salivatory response. *Physiology & Behavior*, *51*, 945-950.
- Estes, W. K., & Skinner, B. F. (1941). Some quantitative properties of anxiety. *Journal of Experimental Psychology*, *29*, 390-400.
- Falk, J. L. (1971). The nature and determinants of adjunctive behavior. *Physiology and Behavior*, *6*, 577-588.
- Flaherty, C. F., & Checke, S. (1982). Anticipation of incentive gain. *Animal Learning & Behavior*, *10*, 177-182.
- Gamzu, E., & Schwartz, B. (1973). The maintenance of key pecking by stimulus-contingent and response-independent food presentation. *Journal of the Experimental Analysis of Behavior*, *19*, 65-72.
- Goodman, D. A., & Weinberger, N. M. (1973). Habituation in "lower" tetrapod vertebrates: Amphibia as vertebrate model systems. In H. V. S. Peeke & M. J. Herz (Eds.), *Habituation. Vol. 1: Behavioral studies* (pp. 85-140). New York: Academic Press.
- Graham, F. K. (1973). Habituation and dishabituation of responses innervated by the autonomic nervous system. In H. V. S. Peeke & M. J. Herz (Eds.), *Habituation. Vol. 1: Behavioral studies* (pp. 163-218). New York: Academic Press.
- Groves, P. M., & Thompson, R. F. (1970). Habituation: A dual-process theory. *Psychological Review*, *77*, 419-450.
- Harris, J. D. (1943). Habitatory response decrement in the intact organism. *Psychological Bulletin*, *40*, 385-422.
- Hearst, E., & Jenkins, H. M. (1974). *Sign-tracking: The stimulus-reinforcer relation and directed action*. Austin, TX: Psychonomic Society.
- Herrnstein, R. J. (1970). On the law of effect. *Journal of the Experimental Analysis of Behavior*, *13*, 243-266.
- Hinde, R. A. (1970). Behavioral habituation. In G. Horn & R. A. Hinde (Eds.), *Short-term changes in neural activity and behavior* (pp. 3-40). Cambridge, England: Cambridge University Press.
- Hinson, J. M., & Staddon, J. E. R. (1983). Hill-climbing by pigeons. *Journal of the Experimental Analysis of Behavior*, *39*, 25-47.
- Hodos, W., & Bonbright, J. C., Jr. (1972). The detection of visual intensity differences by pigeons. *Journal of the Experimental Analysis of Behavior*, *18*, 471-479.
- Humphrey, G. (1930). Extinction and negative adaptation. *Psychological Review*, *37*, 361-363.
- Humphrey, G. (1933). *The nature of learning in its relation to the living system*. London: Kegan Paul, Trench, Trubner.
- Jerome, E. A., Moody, J. A., Connor, T. J., & Ryan, J. (1958). Intensity of illumination and the rate of responding in a multiple-door situation. *Journal of Comparative and Physiological Psychology*, *51*, 47-49.
- Kandel, E., Castellucci, V., Pinsker, H., & Kupfermann, I. (1970). The role of synaptic plasticity in the short-term modification of behavior.

- In G. Horn & R. A. Hinde (Eds.), *Short-term changes in neural activity and behavior* (pp. 281–322). Cambridge, England: Cambridge University Press.
- Kimble, D. P., & Ray, R. S. (1965). Reflex habituation and potentiation in *Rana pipiens*. *Animal Behaviour*, *13*, 530–533.
- Kimmel, H. D. (1973). Habituation, habitability and conditioning. In H. V. S. Peeke & M. J. Herz (Eds.), *Habituation. Vol. 1: Behavioral studies* (pp. 219–238). New York: Academic Press.
- Kling, J. W., & Stevenson, J. G. (1970). Habituation and extinction. In G. Horn & R. A. Hinde (Eds.), *Short-term changes in neural activity and behavior* (pp. 41–61). Cambridge, England: Cambridge University Press.
- Lubow, R. E. (1965). Latent inhibition: Effects of frequency of nonreinforced preexposure of the CS. *Journal of Comparative and Physiological Psychology*, *60*, 454–457.
- Lyon, D. O., & Ozolins, D. (1970). Pavlovian conditioning of shock-elicited aggression: A discrimination procedure. *Journal of the Experimental Analysis of Behavior*, *13*, 325–331.
- Mackintosh, N. J. (1987). Neurobiology, psychology and habituation. *Behaviour Research and Therapy*, *25*, 81–97.
- Mackworth, J. F. (1968). Vigilance, arousal and habituation. *Psychological Review*, *75*, 308–322.
- McCarthy, D., & Voss, P. (1995). Delayed matching-to-sample performance: Effects of relative reinforcer frequency and of signaled versus unsignaled reinforcer magnitudes. *Journal of the Experimental Analysis of Behavior*, *63*, 33–51.
- McSweeney, F. K. (1992). Rate of reinforcement and session duration as determinants of within-session patterns of responding. *Animal Learning & Behavior*, *20*, 160–169.
- McSweeney, F. K., Hatfield, J., & Allen, T. M. (1990). Within-session responding as a function of post-session feedings. *Behavioural Processes*, *22*, 177–186.
- McSweeney, F. K., & Hinson, J. M. (1992). Patterns of responding within sessions. *Journal of the Experimental Analysis of Behavior*, *58*, 19–36.
- McSweeney, F. K., & Johnson, K. S. (1994). The effect of time between sessions on within-session patterns of responding. *Behavioural Processes*, *31*, 207–218.
- McSweeney, F. K., & Roll, J. M. (1993). Responding changes systematically within sessions during conditioning procedures. *Journal of the Experimental Analysis of Behavior*, *60*, 621–640.
- McSweeney, F. K., Roll, J. M., & Cannon, C. B. (1994). The generality of within-session patterns of responding: Rate of reinforcement and session length. *Animal Learning & Behavior*, *22*, 252–266.
- McSweeney, F. K., Roll, J. M., & Weatherly, J. N. (1994). Within-session changes in responding during several simple schedules. *Journal of the Experimental Analysis of Behavior*, *62*, 109–132.
- McSweeney, F. K., Swindell, S., & Weatherly, J. N. (in press-a). Within-session changes in adjunctive and instrumental responding. *Learning and Motivation*.
- McSweeney, F. K., Swindell, S., & Weatherly, J. N. (in press-b). Within-session changes in responding during autoshaping and automaintenance procedures. *Journal of the Experimental Analysis of Behavior*.
- McSweeney, F. K., Weatherly, J. N., & Roll, J. M. (1995). Within-session changes in responding during concurrent schedules that employ two different operanda. *Animal Learning & Behavior*, *23*, 237–244.
- McSweeney, F. K., Weatherly, J. N., Roll, J. M., & Swindell, S. (1995). Within-session patterns of responding when the operandum changes during the session. *Learning and Motivation*, *26*, 403–420.
- McSweeney, F. K., Weatherly, J. N., & Swindell, S. (1995a). Prospective factors contribute little to within-session changes in responding. *Psychonomic Bulletin & Review*, *2*, 234–238.
- McSweeney, F. K., Weatherly, J. N., & Swindell, S. (1995b). Within-session changes in key and lever pressing for water during several multiple variable-interval schedules. *Journal of the Experimental Analysis of Behavior*, *64*, 75–94.
- McSweeney, F. K., Weatherly, J. N., & Swindell, S. (1996). Within-session changes in responding during variable interval schedules. *Behavioural Processes*, *36*, 67–76.
- McSweeney, F. K., Weatherly, J. N., & Swindell, S. (in press). Within-session patterns of responding during delayed matching to sample and discrimination procedures. *Animal Learning & Behavior*.
- Melville, C. L., Rybiski, L. R., & Kamrani, B. (in press). Within-session responding as a function of force required for lever press. *Behavioural Processes*.
- Montgomery, K. C. (1953a). The effect of activity deprivation upon exploratory behavior. *Journal of Comparative and Physiological Psychology*, *46*, 438–441.
- Montgomery, K. C. (1953b). The effect of hunger and thirst drives upon exploratory behavior. *Journal of Comparative and Physiological Psychology*, *46*, 315–319.
- Papini, M. R., & Overmier, J. B. (1985). Partial reinforcement and autoshaping of the pigeon's key-peck behavior. *Learning and Motivation*, *16*, 109–123.
- Patterson, T. L., & Petrinoich, L. (1979). Field studies of habituation: II. Effect of massed stimulus presentation. *Journal of Comparative and Physiological Psychology*, *93*, 351–359.
- Pavlov, I. P. (1927). *Conditioned reflexes*. London: Oxford University Press.
- Peeke, H. V., Avis, H. H., & Peeke, S. C. (1979). Motivational variables and the sensitization and habituation of aggression in the convict cichlid (*Cichlasoma nigrofasciatum*). *Zeitschrift für Tierpsychologie*, *51*, 363–379.
- Petrinoich, L. (1984). A two-factor dual-process theory of habituation and sensitization. In H. V. S. Peeke & L. Petrinoich (Eds.), *Habituation, sensitization and behavior* (pp. 17–55). New York: Academic Press.
- Petrinoich, L., & Patterson, T. L. (1979). Field studies of habituation. I: Effect of reproductive condition, number of trials, and different delay intervals on responses of the white-crowned sparrow. *Journal of Comparative and Physiological Psychology*, *93*, 337–350.
- Petrinoich, L., & Peeke, H. V. S. (1973). Habituation to territorial song in the white-crowned sparrow (*Zonotrichia leucophrys*). *Behavioral Biology*, *8*, 743–748.
- Pinsker, H., Kupfermann, I., Castellucci, V., & Kandel, E. (1970, March 27). Habituation and dishabituation of the gill-withdrawal reflex in *Aplysia*. *Science*, *167*, 1740–1742.
- Poucet, B., Durup, M., & Thinus-Blanc, C. (1988). Short-term and long-term habituation of exploration in rats, hamsters and gerbils. *Behavioural Processes*, *16*, 203–211.
- Rachlin, H. (1973). Contrast and matching. *Psychological Review*, *80*, 217–234.
- Rachlin, H., & Krasnoff, J. (1983). Eating and drinking: An economic analysis. *Journal of the Experimental Analysis of Behavior*, *39*, 385–404.
- Rankin, C. H., & Broster, B. S. (1992). Factors affecting habituation and recovery from habituation in the nematode *Caenorhabditis elegans*. *Behavioural Neuroscience*, *106*, 239–249.
- Razran, G. (1956). Extinction re-examined and re-analyzed: A new theory. *Psychological Review*, *63*, 39–52.
- Roll, J. M., McSweeney, F. K., Johnson, K. S., & Weatherly, J. N. (1995). Satiety contributes little to within-session decreases in responding. *Learning and Motivation*, *26*, 323–341.
- Rubin, H. B., & Brown, H. J. (1969). The rabbit as a subject in behavioral research. *Journal of the Experimental Analysis of Behavior*, *12*, 663–667.
- Schoenfeld, W. N., Antonitis, J. J., & Bersh, P. J. (1950). Uncondi-

- tioned response rate of the white rat in a barpressing apparatus. *Journal of Comparative and Physiological Psychology*, 43, 41-48.
- Siegel, S., & Domjan, M. (1971). Backward conditioning as an inhibitory procedure. *Learning and Motivation*, 2, 1-11.
- Sokolov, Y. N. (1963). *Perception and the conditioned reflex*. (S. W. Waydenfeld, Trans.). Oxford, England: Pergamon Press.
- Staddon, J. E. R., & Simmelhag, V. L. (1971). The "superstition" experiment: A reexamination of its implications for the principles of adaptive behavior. *Psychological Review*, 78, 3-43.
- Stein, L. (1966). Habituation and stimulus novelty: A model based on classical conditioning. *Psychological Review*, 73, 352-356.
- Swithers, S. E., & Hall, W. G. (1994). Does oral experience terminate ingestion? *Appetite*, 23, 113-138.
- Swithers-Mulvey, S. E., & Hall, W. G. (1992). Control of ingestion by oral habituation in rat pups. *Behavioral Neuroscience*, 106, 710-717.
- Swithers-Mulvey, S. E., & Hall, W. G. (1993). Integration of oral habituation and gastric signals in decerebrate rat pups. *American Journal of Physiology*, 265, R216-R219.
- Swithers-Mulvey, S. E., Miller, G. L., & Hall, W. G. (1991). Habituation of oromotor responding to oral infusions in rat pups. *Appetite*, 17, 55-67.
- Swithers-Mulvey, S. E., Mishu, K. R., & Hall, W. G. (1992). Oral habituation in rat pups is in the brainstem. *Physiology & Behavior*, 51, 639-642.
- Thompson, R. F., Groves, P. M., Teyler, T. J., & Roemer, R. A. (1973). A dual-process theory of habituation: Theory and behavior. In H. V. S. Peeke & M. J. Herz (Eds.), *Habituation. Vol. 1: Behavioral studies* (pp. 239-271). New York: Academic Press.
- Thompson, R. F., & Spencer, W. A. (1966). Habituation: A model phenomenon for the study of neuronal substrates of behavior. *Psychological Review*, 73, 16-43.
- Thorpe, W. H. (1966). *Learning and instinct in animals*. Cambridge, MA: Harvard University Press.
- Tomie, A. (1976). Interference with autoshaping by prior context conditioning. *Journal of Experimental Psychology: Animal Behavior Processes*, 2, 323-334.
- Wagner, A. R. (1976). Priming in STM: An information-processing mechanism for self-generated or retrieval-generated depression in performance. In T. J. Tighe & R. N. Leaton (Eds.), *Habituation: Perspectives from child development, animal behavior and neurophysiology* (pp. 95-128). New York: Wiley.
- Weatherly, J. N., & McSweeney, F. K. (1995). Within-session patterns of responding when rats press levers for water: Effects of component stimuli and environment. *Behavioural Processes*, 34, 141-152.
- Weatherly, J. N., McSweeney, F. K., & Swindell, S. (1995). On the contributions of responding and reinforcement to within-session patterns of responding. *Learning and Motivation*, 26, 421-432.
- Weatherly, J. N., McSweeney, F. K., & Swindell, S. (in press). Within-session patterns during conjoint variable-interval variable-time schedules. *Journal of the Experimental Analysis of Behavior*.
- Wilkinson, L. (1990). *SYSTAT: The system for statistics [software]*. Evanston, IL: SYSTAT.
- Williams, J. M., Hamilton, L. W., & Carlton, P. L. (1974). Pharmacological and anatomical dissociation of two types of habituation. *Journal of Comparative and Physiological Psychology*, 87, 724-732.
- Williams, J. M., Hamilton, L. W., & Carlton, P. L. (1975). Ontogenetic dissociation of two classes of habituation. *Journal of Comparative and Physiological Psychology*, 89, 733-737.
- Windsor, A. L. (1930). Experimental extinction and negative adaptation. *Psychological Review*, 37, 174-178.
- Wixted, J. T., & Ebbesen, E. B. (1991). On the form of forgetting. *Psychological Science*, 2, 409-415.

Received September 15, 1995

Revision received January 23, 1996

Accepted January 28, 1996 ■

Low Publication Prices for APA Members and Affiliates

Keeping you up-to-date. All APA Fellows, Members, Associates, and Student Affiliates receive—as part of their annual dues—subscriptions to the *American Psychologist* and *APA Monitor*. High School Teacher and International Affiliates receive subscriptions to the *APA Monitor*, and they may subscribe to the *American Psychologist* at a significantly reduced rate. In addition, all Members and Student Affiliates are eligible for savings of up to 60% (plus a journal credit) on all other APA journals, as well as significant discounts on subscriptions from cooperating societies and publishers (e.g., the American Association for Counseling and Development, Academic Press, and Human Sciences Press).

Essential resources. APA members and affiliates receive special rates for purchases of APA books, including the *Publication Manual of the American Psychological Association*, and on dozens of new topical books each year.

Other benefits of membership. Membership in APA also provides eligibility for competitive insurance plans, continuing education programs, reduced APA convention fees, and specialty divisions.

More information. Write to American Psychological Association, Membership Services, 750 First Street, NE, Washington, DC 20002-4242.