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CRITICISMS OF THE SATIETY HYPOTHESIS AS AN EXPLANATION FOR WITHIN-SESSION DECREASES IN RESPONDING

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The authors of four papers recently reported that satiation provides a better explanation than habituation for within-session decreases in conditioned responding. Several arguments question this conclusion. First, the contribution of habituation to within-session changes in responding seems clearly established. Information that is consistent with habituation, but that is difficult to reconcile with satiation, is not adequately addressed. Second, the limited evidence offered in support of satiation is ambiguous because the results are just as compatible with habituation as with other satiety variables. Finally, the term *satiation* is used in an intuitive way that is sometimes contradicted by research about the termination of ingestion. Use of the technical term *satiation* in a way that differs from its conventional usage will only isolate operant psychology from other areas of psychological research.

Key words: within-session changes in response rates, satiation, habituation, arousal, sensitization

Rate of responding often increases and then decreases within a session when subjects respond on conditioning procedures (e.g., McSweeney, 1992). These within-session changes in responding are produced primarily by changes in the effectiveness of the reinforcer with its repeated presentation in the session (e.g., McSweeney, Hinson, & Cannon, 1996; McSweeney, Weatherly, & Swindell, 1996a). As a result, two ideas have competed to explain the within-session decreases in responding. Killeen (e.g., 1995) argued that animals become satiated to repeatedly presented reinforcers (the satiety hypothesis). McSweeney et al. (1996) argued that subjects habituate to aspects of the experimental procedure that are presented repeatedly (e.g., reinforcers) or for a prolonged time (e.g., the context; the habituation hypothesis). Both satiation and habituation are assumed to reduce the ability of reinforcers to support conditioned responding. The satiety and habituation hypotheses are not entirely independent. As will be discussed below, habituation is thought to be one of many factors that contribute to satiety (e.g., Swithers & Hall, 1994). Nevertheless, distinguishing between the contribution of habituation and the contributions of other satiety factors may be important for both theoretical and applied reasons.

From a theoretical standpoint, within-session changes in operant responding represent a large, reliable, and general behavioral effect (e.g., McSweeney & Roll, 1993). Therefore, a complete theory of operant responding must accurately characterize the factors that produce those changes. In addition, within-session changes may eventually contribute to explaining many poorly understood phenomena in the conditioning literature. Among these phenomena are extinction (McSweeney et al., 1996; McSweeney, Swindell, & Weatherly, 1999), multiple-schedule behavioral contrast (McSweeney & Weatherly, 1998), decreases in response rates at high rates of reinforcement (McSweeney, 1992), the contribution of economic factors to performance (McSweeney, Swindell, & Weatherly, 1996b), and the regulation of motivated behavior (McSweeney & Swindell, 1999b; Roll & McSweeney, 1999). However, the implications of within-session changes for these phenomena will differ if the satiety rather than the habituation hypothesis is correct. Multiple-schedule behavioral contrast will be used to illustrate this point.

Traditionally, behavioral contrast refers to an inverse relation between the rate of re-

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sponding during one component of a multiple schedule and reinforcement in the other component (e.g., McSweeney & Norman, 1979). For example, a multiple variable-interval (VI) 60-s VI 60-s schedule might be changed to a multiple VI 60-s extinction schedule. If rate of responding during the VI 60-s component increased with this worsening of alternative reinforcement, the increase in response rate would be labeled *positive contrast*.

McSweeney and Weatherly (1998) explained positive contrast by arguing that reinforcers retain their effectiveness better across the session (less habituation or satiation) when only approximately 30 reinforcers are presented per hour during the multiple VI 60-s extinction schedule than when approximately 60 reinforcers are presented per hour during the multiple VI 60-s VI 60-s schedule. The more effective reinforcers during the multiple VI 60-s extinction schedule support a higher rate of responding, and faster responding is observed during its VI 60-s component than during the same component of the multiple VI 60-s VI 60-s schedule.

This explanation of contrast is simple and relies only on phenomena that have been demonstrated by independent research. However, the experimental tests of this idea will differ if repeatedly presented reinforcers lose their effectiveness through satiation rather than through habituation. If the habituation hypothesis is correct, then manipulations that slow habituation should produce positive contrast. For example, positive contrast should be produced by manipulations such as reducing exposure to the stimulus by decreasing its size (e.g., Thompson & Spencer, 1966), by introducing dishabituating stimuli such as lights or noises (e.g., Thompson & Spencer, 1966), or by making unpredictable changes in the reinforcer (e.g., Swithers & Hall, 1994). On the other hand, if the satiety hypothesis is correct, then positive contrast should be produced by manipulations that reduce the contribution of other satiety variables. Such manipulations include decreasing the size or caloric content of the reinforcer (e.g., Mook, 1996).

From an applied standpoint, the loss of effectiveness that occurs when reinforcers are repeatedly presented may be undesirable when operant techniques are used to correct behavioral problems. The manipulations that can be used to reduce this loss, or to restore reinforcer effectiveness after it has been lost, will differ depending on whether the habituation or satiety hypothesis is correct. Again, if habituation is responsible, then these manipulations will include introducing dishabituators. If other satiety variables are responsible, then these manipulations will include reducing reinforcer size or caloric content.

The authors of four papers recently argued that satiation provides a better explanation than habituation for within-session decreases in responding (Bizo, Bogdanov, & Killeen, 1998; DeMarse, Killeen, & Baker, 1999; Hinson & Tennison, 1999; Palya & Walter, 1997). The present paper examines their arguments. We begin by defining our terms, because a discussion of definitions may help to clarify the issues. We then argue that three problems plague the satiety hypothesis. First, it is inconsistent with many empirical results that are consistent with the habituation hypothesis. Second, the evidence that has been offered to support the satiety hypothesis is ambiguous, because it is just as compatible with habituation as it is with other satiety variables. Third, the satiety hypothesis, as offered in these papers, is based on an intuitive, not an empirical, understanding of satiety.

DEFINITIONS

The use of the terms *satiation* and *habituation* in the operant literature should be consistent with past research on each of these topics. If our definitions are consistent, then we can use information gathered in the past to identify factors that should alter within-session changes in operant responding. If our definitions are not consistent, then our idiosyncratic language will isolate us from other areas of psychological research. No definition of either satiation or habituation would be universally accepted by all researchers on these topics (e.g., Savory, 1988; Weingarten, 1985). However, the definitions that follow are compatible with the way these terms are used by the researchers who study them.

Habituation

Habituation is often defined as a decrease in responsiveness to a stimulus when that stimulus is presented repeatedly or for a pro-

Table 1

A tentative list of the empirical characteristics of habituation. Characteristics that are preceded by asterisks were included in Thompson and Spencer's (1966) list of these characteristics. Examples of references that establish the role of other characteristics are listed.

*1. Spontaneous recovery: Responsiveness to a habituated stimulus recovers when that stimulus is not presented for a time.
2. Stimulus specificity (e.g., Swithers & Hall, 1994; Whitlow, 1975): Habituation is disrupted by unpredictable changes in the presented stimulus.
3. Variety effects (e.g., Broster & Rankin, 1994): Perhaps because of stimulus specificity, habituation occurs more slowly to stimuli that are presented in a variable, rather than a fixed, manner (e.g., after variable, rather than fixed, interstimulus intervals).
*4. Dishabituation: Presenting a strong, different, or extra stimulus restores responsiveness to a habituated stimulus. Although dishabituation is listed here as a characteristic of habituation, researchers disagree about whether the return of responsiveness occurs because habituation decreases (e.g., Marcus, Nolen, Rankin, & Carew, 1988) or because sensitization is added (e.g., Groves & Thompson, 1970; see the discussion of sensitization below).
*5. Dishabituation habituates: Repeated presentation of dishabituators reduces their ability to restore habituated responding.
*6. Stimulus rate: Faster rates of stimulus presentation yield faster and more pronounced habituation than slower rates.
7. Stimulus rate and recovery: Spontaneous recovery may be faster after faster than after slower rates of stimulus presentation (Staddon & Higa, 1996).
*8. Stimulus exposure: Responsiveness to a repeatedly presented stimulus decreases with increases in stimulus exposure.
9. Long-term habituation (e.g., Wagner, 1976): Spontaneous recovery may be incomplete. Some habituation is learned and persists over time.
*10. Repeated habituations: Perhaps because of long-term habituation, habituation may become more rapid with repeated habituation followed by spontaneous recovery.
*11. Stimulus intensity: Habituation is sometimes, but not always (e.g., Groves & Thompson, 1970), faster and more pronounced for less intense than for more intense stimuli.
12. Generality (e.g., Thorpe, 1966): Habituation occurs for most, if not all, species of animals. It also occurs for most stimuli, including those that have no ingestive consequences (e.g., lights, noises). The exact rate of habituation differs depending on the species, the stimulus, the response used as a measure, and the individual subject (e.g., Hinde, 1970).

Habituation is often accompanied by "sensitization" (e.g., Groves & Thompson, 1970). Therefore, if habituation occurs, then the following phenomena might also be observed:

13. Sensitization by early-stimulus presentations (e.g., Groves & Thompson, 1970): An increase (sensitization), rather than a decrease (habituation), in responsiveness may occur to a repeatedly presented stimulus during its first few presentations.
14. Sensitization by stimuli from another modality (e.g., Swithers & Hall, 1994): An increase in responsiveness to a stimulus may be produced by the introduction of a stimulus from another modality (e.g., a light or noise). Both sensitization and dishabituation (Characteristic 4) may involve the introduction of a stimulus from another modality. Results are conventionally described as dishabituation if the stimulus restores responsiveness to an already habituated stimulus and as sensitization if the stimulus from another modality increases responding before substantial habituation occurs to the other stimulus (e.g., Marcus et al., 1988).

longed time (e.g., Groves & Thompson, 1970). Thompson and Spencer (1966) also argued that conformity to a list of empirical properties could be used as an elaborate operational definition of habituation. Since the time of their paper, some of the empirical characteristics that they offered have been questioned (e.g., the effect of stimulus intensity, e.g., Groves & Thompson); some are considered to be of less generality (e.g., habituation below zero, e.g., Wyers, Peeke, & Herz, 1973); and others have been added to the list (e.g, sensitization, Groves & Thompson; stimulus specificity, Swithers & Hall, 1994). Nevertheless, in the habituation literature, a decrease in responsiveness to a repeatedly presented stimulus is usually considered to be habituation when it conforms to a generally accepted list of empirical properties (e.g., Leaton & Tighe, 1976; Teyler, Chiana, DiScenna, & Roemer, 1984).

Table 1 contains a tentative list of the empirical characteristics of habituation. Again, although there is general agreement on the properties of habituation (e.g., Baker & Tiffany, 1985), individual researchers might omit some of the characteristics listed in Table 1 or include others. Decreases in respon-

siveness are usually called habituation even if those decreases fail to show all of these characteristics. For example, most researchers would consider the decline in gill withdrawal in *Aplysia* with the repeated presentation of a tactile stimulus to be a clear example of habituation. However, by one count, gill withdrawal shows only six of Thompson and Spencer's (1966) original nine characteristics of habituation (Kandel, Castellucci, Pinsker, & Kupfermann, 1970).

Satiation

Satiation usually refers to a decline in the consumption of an ingestive stimulus (e.g., food, water) with its repeated consumption. The factors that contribute to the decline in consumption are called satiety factors. Lists of empirically identified satiety factors appear in many textbooks. For example, the index of Mook (1996) lists the topic of ''satiety (satiation) of feeding'' (p. 633). The pages referred to in this citation (pp. 76–79) list the following satiety factors for food: oral stimulation; distension of the stomach; distension of the duodenum; increases in blood sugar level at the liver; and increases in cholecystokinin (CCK) in the blood. Again, agreement among all researchers on any particular list of satiety factors would be imperfect, although it would be substantial. Mook's textbook was used to provide the present example because his own research is devoted to understanding satiety.

The list of satiety factors would also depend on the ingestive stimulus that was studied (e.g., food vs. water). Throughout this paper, we will use satiety to food as an example because most, but not all (e.g., McSweeney, Weatherly, & Swindell, 1995b), studies of within-session changes in responding use food as a reinforcer. However, the specific predictions of the satiety hypothesis would be somewhat different if a different reinforcer was used.

In the past, the study of satiety focused mainly on postingestive factors. That is, it focused on factors that occur after food has been digested by the stomach. More recent research has recognized the importance of oral factors. Habituation to the sensory properties of the ingestive stimulus is one of those oral factors (e.g., Epstein, Rodefer, Wisniewski, & Caggiula, 1992; McSweeney & Swindell, 1999b; Swithers & Hall, 1994). This may introduce confusion, because studies that allow an animal to consume food orally produce both habituation to the food through exposure to its sensory properties and changes in other satiety factors as a result of ingestion. The contribution of these different factors must be separated before any changes in behavior can be clearly attributed to a particular variable.

Throughout this paper we assume that those who favor the satiety hypothesis argue that satiety factors other than habituation play a role in producing within-session changes in operant responding. If they assumed that habituation was the primary contributor to within-session changes, then they would agree with the habituation hypothesis, but they do not (e.g., Bizo et al., 1998; DeMarse et al., 1999; Hinson & Tennison, 1999; Palya & Walter, 1997).

Separating the Satiety and Habituation Hypotheses

Habituation is usually classified as an oral factor because satiety research has shown that habituation to oral stimuli contributes to the termination of feeding in rats and humans (e.g., Epstein et al., 1992; Swithers & Hall, 1994). The precise nature of the stimuli to which subjects habituate when consuming food, however, has not been experimentally identified. The emphasis on oral factors probably arose because satiety research usually uses rats and humans as subjects. It seems reasonable that oral factors should contribute for species that rely on taste and smell to govern ingestion rather than on other sensory systems (e.g., vision). The emphasis on oral factors may be less appropriate for other species. For example, highly visual animals, such as birds, might habituate primarily to visual characteristics of food (e.g., its color or size). Even rats might habituate to stimuli that are not oral. For example, although this is speculative, the location of food might be part of the stimulus to which subjects habituate for many species.

On the assumption that subjects mainly habituate to the oral properties of food when they consume that food, physiological manipulations may be used to separate the contribution of habituation from the contributions of other satiety factors. For example, sham

feeding procedures that shunt food from the body before it reaches the stomach should produce habituation (e.g., to the taste and texture of the food) without any contribution by postingestive satiety factors (e.g., stomach distension, changes in CCK and blood glucose levels) because food never reaches the stomach. In contrast, intubation of food directly into the stomach should produce postingestive satiety factors without any contribution of oral factors because the food bypasses the mouth. (See Mook, 1996, pp. 76–79, for studies that used these methods to isolate satiety factors.)

This physiological approach is not entirely satisfactory, however. First, the assumption that subjects habituate only to the oral properties of food when consuming that food may be incorrect. Therefore, subjects may be exposed to, and habituate to, other sensory properties of food (e.g., its temperature) even when food bypasses the mouth. Second, several satiety factors might be located in the mouth. In that case, studies showing that ingestion terminated when food entered the mouth but immediately exited the body would remain ambiguous. Ingestion might have been terminated by, for example, a fixed number of bites rather than by habituation. Finally, the behavior of a physiologically altered animal may differ from that of the intact animal.

As a result, our research has focused primarily on a second means of separating the contribution of habituation from that of other satiety factors. The empirical properties of habituation can be used to identify situations in which the predictions of habituation differ from those of other satiety variables. For example, increasing the caloric content of the food should increase blood glucose levels and therefore, produce faster satiety for a calorie-regulating animal such as the rat (e.g., Adolph, 1947; Hausmann, 1933). In contrast, increasing the caloric content of the food might reduce habituation if it increased stimulus intensity (i.e., perceived sweetness). Habituation is sometimes (e.g., Thompson & Spencer, 1966), but not always (e.g., Groves & Thompson, 1970), slower for more than for less intense stimuli. Table 2 provides more examples of these situations.

EVIDENCE FAVORING THE HABITUATION OVER THE SATIETY HYPOTHESIS

McSweeney et al. (1996) and McSweeney and Roll (1998) showed that the empirical characteristics of within-session changes in responding are strikingly similar to the empirical characteristics of habituation. Their arguments will not be repeated here, except to state that all of the empirical characteristics of habituation listed in Table 1 have been shown for within-session changes in responding except Characteristics 5 (dishabituation habituates), 7 (spontaneous recovery is faster after stimuli are presented at higher rates), and 14 (sensitization by stimuli from another modality). These characteristics have yet to be studied. Some demonstrations of the characteristics of habituation were true predictions because they were confirmed only after the habituation hypothesis predicted them. Researchers have applied the term *habituation* to phenomena that share as few as three of the empirical characteristics of habituation (e.g., Eisenstein & Peretz, 1973). Because conformity to the empirical characteristics of habituation is used as an operational definition of the term (e.g., Thompson & Spencer, 1966), the contribution of habituation to within-session changes in responding has been established by typical standards of researchers who study habituation.

Do other satiety variables also contribute to producing the within-session changes in responding? Table 2 summarizes some evidence that bears on this question. It presents a finding, lists some of the studies that support that finding, and then classifies whether the finding is consistent with the habituation hypothesis, with the satiety hypothesis, or with both. Asterisks indicate findings on which the interpretation listed in Table 2 disagrees with the interpretation given in one of the four papers that favor the satiety hypothesis (Bizo et al., 1998; DeMarse et al., 1999; Hinson & Tennison, 1999; Palya & Walter, 1997). Table 2 does not provide a complete summary of research on within-session changes in responding. Many such studies do not bear on the distinction because they preceded the arguments over satiation versus habituation. Table 2 presents only those studies that may be

Table 2

Findings that have been reported for within-session changes in responding; some of the references that support that conclusion; and whether the conclusion is predicted by the habituation or satiety hypotheses. Asterisks indicate findings for which our classification of the evidence differs from that given by the authors of at least one study that reports that finding. When these studies are consistent with a characteristic of habituation as listed in Table 1, the number of that characteristic is given in parentheses after the finding.

Finding	Habituation	Satiation
Retrospective, not prospective, factors produce the decreases in responding McSweeney, Weatherly, and Swindell (1995a)	x	x
A decrease in reinforcer effectiveness contributes to the decreases in responding McSweeney, Weatherly, and Swindell (1996a)	x	x
The decreases are usually steeper for higher than for lower rates of reinforcement (6) McSweeney (1992) McSweeney, Roll, and Cannon (1994) McSweeney, Roll, and Weatherly (1994) McSweeney and Swindell (1999a) McSweeney, Swindell, and Weatherly (1996a) McSweeney, Weatherly, and Swindell (1995b) McSweeney, Weatherly, and Swindell (1996b)	x	x
*The decreases are steeper for smaller or smaller cropped animals Bizo, Bogdanov, and Killeen (1998) DeMarse, Killeen, and Baker (1999) Hinson and Tennison (1999) Palya and Walter (1997)	x	x
*The decreases may be steeper for larger (longer) than for smaller (shorter) food (8) Bizo et al. (1998) Cannon and McSweeney (1995) DeMarse et al. (1999) Palya and Walter (1997) Roll, McSweeney, Johnson and Weatherly (1995)	x	x
*The decreases may differ for qualitatively different reinforcers (12) Bizo et al. (1998) McSweeney, Swindell, and Weatherly (1996b) McSweeney, Weatherly, and Swindell (1996a)	x	x
*The decreases are steeper when animals are prefed and the food is eaten (8) DeMarse et al. (1999)	x	x
The decreases are not changed by prefeedings when food is intubated (8) Roll et al. (1995)	x	
*Frequent and unpredictable changes in external stimuli reduce the decreases (4) Hinson and Tennison (1999)	x	
The decreases may be steeper for lower calorie (or less) than for higher calorie (or more) food (11) Melville, Rue, Rybiski, and Weatherly (1997) Melville and Weatherly (1996) Weatherly, McSweeney, and Swindell (1997)	x	
Increasing the caloric content of food may not steepen the decrease Roll et al.	x	
An increase in the amount of delivered food may increase, rather than decrease, response rate for the original reinforcer (4) Aoyama and McSweeney (in press) Ernst (2000) McSweeney and Roll (1998)	x	

Table 2
(*Continued*)

Finding	Habituation	Satiation
Changing the reinforcer increases response rate even if the amount or value of reinforcement increases with the change (2) Ernst (2000) Rybiski (1996)	x	
Increasing reinforcer variety reduces the steepness of the decrease[a] (3) Aoyama and McSweeney (in press) Ernst (2000) Facon and Darge (1996) McSweeney, Hinson, and Cannon (1996) Melville et al. (1997)	x	
The decreases may occur for noningestive reinforcers (e.g., lights) (12) Facon and Darge (1996) Kish (1966) for a review	x	
Repeatedly delivered aversive stimuli also lose their effectiveness (12) Azrin (1960) Jerome, Moody, Connor, and Ryan (1958)	x	
The decreases may occur when no reinforcers are presented (12) McSweeney, Swindell, and Weatherly (1999) Schoenfeld, Antonitis, and Bersh (1950)	x	
The decreases may change when the total food delivered is held constant Weatherly, McSweeney, and Swindell (1995)	x	
Changing food deprivation may not change the late-session decrease in responding for food Roll et al. (1995)	x	

[a] Introducing variety slows both habituation and satiation. For example, habituation may be slower when the stimuli are presented at variable, rather than at fixed, interstimulus intervals (Broseter & Rankin, 1994). Animals also eat or drink more when given access to a variety of foods or liquids than when given access to only one (Berry, Beatty, & Klesges, 1985; Clifton, Burton, & Sharp, 1987; Rolls, Rolls, & Rowe, 1980; Rolls et al., 1981; Treit, Spetch, & Deutsch, 1983). In spite of the effect of variety on satiation, we have not listed variety effects as a prediction of the satiety hypothesis because the variety effects in the satiety literature are produced by sensory factors such as habituation rather than by other satiety variables. For example, variety effects can occur when stimuli differ only in their sensory properties such as color or shape (Rolls, Rowe, & Rolls, 1982). They also occur when the food items have no nutritive value (Rolls, Wood, & Rolls, 1980).

useful in comparing the satiety and habituation hypotheses.

Table 2 shows that many findings are compatible with both the habituation and satiety hypotheses. Table 2 also lists 12 findings that pit the predictions of habituation against those of other satiety variables. These predictions seem to fall into three general categories. First, only the habituation hypothesis correctly predicts that within-session changes in responding may be observed when noningestive stimuli (e.g., lights, aversive stimuli) are repeatedly presented. Second, only the habituation hypothesis correctly predicts that response rates sometimes increase, rather than decrease, when the size or caloric content of the reinforcer increases (e.g., as a result of dishabituation). Third, only the habituation hypothesis correctly predicts that the decreases in operant responding can be altered by changing variables that should not alter other satiety variables (e.g., introducing stimuli from another modality).

Some of the findings reported in Table 2 might be reconciled with the satiety hypothesis. For example, adding the concept of arousal might allow the satiety hypothesis to account for the effect of manipulations such as changing the nature of the reinforcer or introducing frequent and unpredictable changes in stimuli from another modality. Killeen and his colleagues have argued that the

repeated presentation of reinforcers may increase response rate by producing arousal (e.g., Killeen, Hanson, & Osborne, 1978) as well as decrease response rate through satiation (e.g., Killeen, 1995). Just as habituation has a companion process, sensitization, satiation may have a companion process, arousal.

However, sensitization has several advantages over arousal as an explanatory variable. First, researchers studying habituation were compelled to postulate the concept of sensitization by the results of their studies (e.g., Groves & Thompson, 1970). The postulation of arousal as a companion process for satiation arose from the study of operant responding (e.g., Killeen et al., 1978), not the study of satiety. Second, sensitization has been studied extensively. Results of this research were used to predict the manipulations that should reduce habituation and, therefore, alter within-session changes in responding. In contrast, the properties of arousal, as a companion process to satiety, have been studied much less. Explicitly specifying the properties of this sort of arousal is important because the term *arousal* has been used in a variety of conflicting ways (e.g., Anderson, 1990; Duffy, 1962; Neiss, 1988). Third, even if the properties of arousal were established, those properties would have to be similar to the properties of sensitization to account for results in Table 2. If the two concepts make the same predictions, then they may just name the same process.

Many of the findings listed in Table 2 are incompatible with the satiety hypothesis because they are inconsistent with research on the termination of ingestion. These findings may be considered crucial experiments that separate the satiety and habituation hypotheses. Because many of the findings in Table 2 were discussed by McSweeney and Roll (1998), we will describe only two here.

First, Melville, Rue, Rybiski, and Weatherly (1997) reported that rats' responding sometimes decreased more steeply late in the session when less concentrated, rather than more concentrated, sucrose solutions served as reinforcers. Such a finding is consistent with habituation, which may be faster and more pronounced for less than for more intense stimuli (Characteristic 11, Table 1; e.g., Thompson & Spencer, 1966). Decreasing the caloric content of a sucrose solution might decrease the intensity of its sweet taste. This finding is the opposite of the prediction of the satiety hypothesis. Food ingestion should terminate faster for higher than for lower calorie solutions for animals, such as rats, that regulate calories (e.g., Adolph, 1947; Hausmann, 1933).

Although Bizo et al. (1998) questioned the interpretation of data that are reported in terms of proportions of total-session responses, Melville et al.'s (1997) conclusion survives a conversion to response rates. For example, if the steepness of the decrease in operant response rate is measured by the difference between the number of responses emitted during the 5-min intervals of the session that contained the highest and the lowest number of responses, the decrease was 76.5 responses for the 1% sucrose solution, 66.0 responses for the 5% solution, and 59.0 responses for the 15% sucrose solution. (See Melville & Weatherly, 1996, and Weatherly, McSweeney, & Swindell, 1997, for additional evidence that the decreases in operant responding may be steeper when less rather than more food is given.)

Second, McSweeney and Roll (1998) reported that changing the reinforcer for a brief time late in the session increased response rate once the orginal reinforcer was restored. The increase in responding occurred regardless of whether the change was an increase or a decrease in the amount of reinforcement delivered and regardless of whether the change produced an increase or a decrease in response rate while it was in effect. These results are consistent with habituation. Changes in the reinforcer should produce dishabituation (Characteristic 4, Table 1; e.g., Thompson & Spencer, 1966). Because dishabituation should restore responsiveness to the habituated stimulus, response rate should increase. This finding contradicts what would be expected from satiety factors such as stomach distension and blood glucose levels. Providing more reinforcers should increase both of these factors and decrease, not increase, response rate. These results were replicated by Aoyama and McSweeney (in press) and by Ernst (2000) using fixed- and variable-ratio schedules as the baseline schedules of reinforcement. Therefore, the results have some generality and are not explained by the disinhibition of any inhibition that

might occur during the fixed-interval schedule baselines used by McSweeney and Roll (e.g., Staddon, 1967).

Some other results that favor the habituation over the satiety hypothesis are equally difficult to dismiss. Table 2 shows that several of these conclusions are supported by more than one study. The studies often come from different laboratories. The studies also often examine the behavior of both rats and pigeons responding in several different conditions. Examining the behavior of two species eliminates many potential procedural criticisms. For example, Bizo et al. (1998) questioned whether our food hoppers for pigeons really provided different access to food when reinforcer duration was varied. Although their criticism might explain why we sometimes failed to find a change in the within-session response pattern when we manipulated reinforcer size for pigeons (e.g., Cannon & McSweeney, 1995), it cannot explain why we found similar results for rats (e.g., Roll, McSweeney, Johnson, & Weatherly, 1995).

ARGUMENTS FOR THE SATIETY HYPOTHESIS ARE COMPATIBLE WITH HABITUATION

The findings in Table 2 that are preceded by an asterisk have been interpreted as supporting the satiety hypothesis by Bizo et al. (1998), DeMarse et al. (1999), Palya and Walter (1997), or Hinson and Tennison (1999). However, these results are at least as consistent with the habituation hypothesis as they are with the satiety hypothesis.

Crop Capacity Correlated with the Decrease in Responding

Three studies measured the amount that subjects ate under free-feeding conditions (Bizo et al., 1998; DeMarse et al., 1999) or close to free-feeding conditions (DeMarse et al.; Hinson & Tennison, 1999). The amount consumed was labeled *capacity* or *crop capacity*. It was assumed that the same amount of food should produce more satiety in birds that have a smaller capacity. If satiation produces the decreases in operant response rates, those decreases should be steeper for subjects with smaller capacities. This prediction was confirmed.

In a related argument, Palya and Walter (1997) showed that within-session decreases in responding are steeper for smaller than for larger birds. They argued that this result is consistent with the satiety hypothesis if smaller birds became satiated more quickly than larger birds. Palya and Walter's finding will not be directly addressed because Bizo et al. (1998) and DeMarse et al. (1999) failed to replicate it. However, the following criticism applies to Palya and Walter's reasoning as well as to that of the other studies.

The reasoning behind these arguments is flawed. To begin with, the authors interpret a correlation (i.e., that body size or amount eaten under free-feeding conditions is correlated with the steepness of the decrease in operant response rate) as causation (e.g., "Satiation Causes Within-Session Decreases in Instrumental Responding" is the title of the article by Bizo et al., 1998). Drawing causal conclusions from correlational data is logically incorrect. When two variables are correlated, either one could cause the other or the correlation could be caused by a third variable.

It has been argued that statistical relations, including correlations, may suggest causation if certain conditions are met (e.g., Susser, 1973). Although it is beyond the scope of the present paper, these conditions are strict (e.g., Susser, p. 142) and do not appear to be met by the data presented for the satiety hypothesis. Nevertheless, assume that these correlations can be interpreted as causation. Even in that case, the causal variable is just as likely to be habituation as it is to be other satiety variables. When the authors argue that crop capacity is correlated with the decreases in operant responding, they seem to be reporting a relation between two independent phenomena (i.e., the physical size of the crop and the behavior of the animal). What they have actually done is measured feeding in two different situations (the home cage and the operant enclosure). Because the subjects consumed food orally when both crop capacity and the decreases in operant responding were measured, many factors were affected, including habituation because the subjects were repeatedly exposed to the sensory properties of food (e.g., Epstein et al., 1992; Swithers & Hall, 1994). Without other evidence, there is no logical basis for attributing the

correlation to any particular satiety factor. Habituation to the sensory properties of the food provides as plausible an explanation of the correlation as any other satiety factor.

Steeper Decreases for Longer Reinforcers

Three studies showed that within-session decreases in operant responding are steeper or operant response rates are slower when subjects are given longer rather than shorter durations of access to food per reinforcer (Bizo et al., 1998, Experiment 1; DeMarse et al., 1999, Experiment 2; Palya & Walter, 1997, Experiment 2). Again, however, as acknowledged by Bizo et al., habituation provides just as plausible an explanation as other satiety variables. Subjects received greater exposure to the sensory properties of the food during longer than during shorter reinforcers. Habituation usually increases with increases in stimulus exposure (Characteristic 8, Table 1; e.g., Thompson & Spencer, 1966).

Different Grains Produce Different Decreases in Responding

Bizo et al. (1998, Experiment 2) reasoned that if satiation produces decreases in operant response rate, then those decreases should be steeper for larger than for smaller grains. They showed that decreases are steeper for popcorn than for milo. Again, however, finding different decreases for different grains may be compatible with the habituation hypothesis. The rate of habituation depends on the nature of the stimulus delivered (Characteristic 12, Table 1; e.g., Hinde, 1970). Therefore, rate of habituation is likely to differ for popcorn and milo.

Rate of habituation may differ for different grains, but one could still argue that the habituation hypothesis does not explicitly predict faster decreases for popcorn than for milo. This is correct, but Bizo et al. (1998) provide no evidence that the satiety hypothesis makes this prediction either. The study by Ploog and Zeigler (1996) that they cite indicates that pigeons peck faster during conditioning procedures for larger than for smaller grain reinforcers. It does not show that pigeons terminate consumption (become satiated) faster for larger than for smaller grains or that this faster termination results from a variable other than habituation (e.g., from crop or stomach distension).

Prefeeding Animals Reduces Response Rate

DeMarse et al. (1999, Experiment 3) reasoned that feeding subjects before the session should increase satiety. They fed the pigeons 0, 5, 15, or 25 g of milo prior to the session and reported that response rates decreased with increases in the amount prefed.

Again, these data are just as compatible with the habituation hypothesis as they are with the satiety hypothesis. Because the food consumed before the session was similar to the food used as a reinforcer, prefeeding exposed the subjects to the sensory properties of that food. Therefore, subjects should have entered the session more habituated to the food when they were prefed than when they were not. Larger prefeedings should mean more sensory exposure and, therefore, more habituation (Characteristic 8, Table 1; e.g., Thompson & Spencer, 1966).

Although Experiment 2 of Roll et al. (1995) was not discussed by DeMarse et al. (1999), this experiment also examined the effect of prefeeding. The rats in Roll et al. responded on a multiple VI 60-s VI 60-s schedule during baseline when no prefeedings were given. The amount of condensed milk reinforcer consumed up to the point in the session at which the peak response rate occurred was calculated for each rat to determine the amount of food required to initiate ''satiation.'' Subjects were then divided into two groups that received either 1.0 or 2.0 times their predetermined amount of milk immediately before the session. Unlike the DeMarse et al. study, the prefeeding was given by intubating food directly into the stomach. Roll et al. reported that prefeeding the rats this way did not alter the within-session pattern of responding for either group.

Roll et al.'s (1995) results are consistent with the habituation hypothesis, but they may not be consistent with the satiety hypothesis. Because the prefeeding food was intubated rather than eaten, the subjects could not habituate to the oral properties of that food (e.g., its taste and texture). In contrast, intubations should produce some satiety because food placed in the stomach alters known satiety factors such as stomach distension, blood glucose levels, and so on. Therefore, the prefeedings should steepen the within-

session decrease in responding if those decreases are produced by satiety. A steepening of the decreases was not observed.

Roll et al.'s (1995) results may be criticized. For example, intubation is an intrusive procedure that may not correctly represent an animal's normal feeding. Nevertheless, these results deserve discussion because physiological interventions such as intubation are frequently used to separate the contributions of pre- and postingestion satiety factors (e.g., Mook, 1996). The habituation hypothesis is consistent with the results of both DeMarse et al. (1999) and Roll et al. The satiety hypothesis is consistent only with the results of DeMarse et al.

Hinson and Tennison (1999)

In a series of four experiments, Hinson and Tennison (1999) failed to find within-session decreases in responding when they provided rates of reinforcement similar to those that usually produce these decreases (e.g., McSweeney, 1992). They concluded that their results support the satiety hypothesis because a measure of capacity (i.e., consumption) predicted the presence of a decrease in responding when such a decrease did occur. As argued earlier, finding a correlation between consumption (i.e., capacity) and the decrease in responding provides no support for the satiety over the habituation hypothesis. Once this argument is dismissed, Hinson and Tennison's results are more consistent with the habituation hypothesis than with the satiety hypothesis.

Habituation provides an obvious explanation for Hinson and Tennison's (1999) findings. They used a complicated discrimination procedure in which visual stimuli changed approximately every 5 to 30 s in different conditions. The newly introduced stimulus was unpredictable and was sometimes drawn from a large set (e.g., 10 or 12 stimuli). In addition, the stimuli were sometimes flickering rather than constant lights. The introduction of these visual stimuli should produce dishabituation (Characteristic 4, Table 1) for a highly visual animal such as a pigeon. Although subjects may habituate to dishabituators (Characteristic 5, Table 1), these particular visual stimuli should retain their effectiveness as dishabituators throughout the session because stimulus changes were frequent and unpredictable (Characteristics 2 and 3, Table 1). Dishabituation by the frequently changing visual stimuli should reduce habituation to the reinforcers and reduce the size of the within-session decrease in responding. This was the result reported by Hinson and Tennison.

In contrast, the satiety hypothesis provides little reason to expect different results in Hinson and Tennison's (1999) experiments than in past studies that provided similar conditions of reinforcement. When the characteristics of the reinforcers (e.g., their size, rate of delivery, etc.) are held constant, satiety factors such as stomach distension, blood glucose levels, and so on should also be constant. Introducing external stimuli, such as lights, should not alter these satiety variables.

Hinson and Tennison (1999) recognized that a factor such as dishabituation might account for their results. They state that their multiple and rapidly changing stimuli might maintain "attention" to the stimulus and therefore, eliminate habituation. However, their use of the term *attention* is questionable. The results of past research can be used to predict that dishabituation will occur in this situation. Dishabituation is usually thought of as either a release from habituation or the introduction of sensitization (Table 1). It is not equated with the maintenance of attention, a concept with very different implications. For example, attention is often assumed to be a limited resource, so that greater attention to some stimuli means less attention to other stimuli (e.g., Hinson & Cannon, 1999). Dishabituation and sensitization are not limited in this way.

The Use of Proportions

Bizo et al. (1998) reasoned that the arguments supporting the habituation hypothesis are flawed because they are often based on proportions of total-session responses rather than on response rates. They are correct that proportions may sometimes lead to different conclusions than do response rates. Examples may be found in the Appendix of McSweeney and Roll (1998). However, there is no a priori reason to assume that response rates provide a "truer" description of behavior than do response proportions. Neither measure has logical priority because both are calculated by dividing number of responses by another measure (session time or total-session re-

sponses). Instead, McSweeney and Roll suggest deciding between these measures by asking which is the most orderly. They then showed that proportions, not response rates, bring order to the data.

In addition, the statistical tests reported in our studies were almost always applied to response rates rather than to proportions. Proportions are bounded and must sum to 1 in violation of the assumptions of some statistical tests. Our conclusions were based on the results of statistical tests on response rates as well as on a visual analysis of response proportions. Therefore, our conclusions almost always apply to data analyzed as response rates, not just as response proportions.

AN INTUITIVE TREATMENT OF SATIATION

Operant researchers should use the terms *satiation* and *habituation* in a manner that is consistent with the research from which the terms arise. Instead, the arguments in support of the satiety hypothesis seem to be based on intuition rather than on an empirical understanding of satiety.

To begin with, the experimental manipulations used differ from those usually used to identify satiety factors. For example, the difference in the within-session decreases in responding for popcorn and milo (Bizo et al., 1998) might arise from any of the many dimensions on which popocorn and milo differ (weight, size, shape, color, texture, taste, caloric content, nutrient composition, topography of the response required for eating, etc.). Even if we did know what variable was responsible (e.g., size), we would not know whether that variable had its effect through habituation (e.g., subjects habituate faster to larger grains because they provide greater sensory exposure) or through other satiety factors (e.g., larger grains produce greater crop or stomach distension). Better tests of the satiety hypothesis would directly manipulate variables that are clearly identified with particular satiety factors (e.g., caloric content, stomach distension).

Research on the termination of food consumption also contradicts an argument offered by Bizo et al. (1998). Roll et al. (1995) showed that deprivation for food does not alter the within-session pattern of responding for food reinforcers. They argued that such a result questions satiation because deprivation should alter the rate of satiety. Bizo et al. disagree. They state that ''the slope of within-session responding should not be expected to change when deprivation level is manipulated. All deprivation does is change the initial level of responding'' (p. 446). Because they do not cite references, it is unclear what data led to that conclusion. Contrary to their argument, however, changing deprivation does alter the changes in eating rate that occur within a meal (i.e., the slope), not just the initial rate of eating (e.g., Bousfield, 1935; Bousfield & Elliott, 1934; Kissileff & Thornton, 1982; Savory, 1988). In fact, at least one study reported that deprivation alters the slope but not the initial rate of eating, which is the opposite of Bizo et al.'s conclusion (e.g., Aoyama, 2000).

As a final point, the factors that produce satiety differ for different species. For example, calories play no role in regulating the consumption of food by the blowfly (e.g., Dethier, 1962, 1976) even though they play a large role in regulating consumption by rats and humans (e.g., Adolph, 1947; Hausmann, 1933). It is therefore noteworthy that all four of the studies that support the satiety hypothesis used pigeons as subjects. On the surface, pigeons seem to be a natural choice because they have been used frequently in studies of within-session changes in responding. But pigeons are not a good choice of subject if one is primarily interested in the role of satiety in producing those changes. Research on the termination of ingestion usually examines the behavior of rats and humans. Less is known about the termination of ingestion in the pigeon. The particular factors that contribute to satiety must be indentified before it can be asked if those factors also contribute to the production of within-session changes in responding. As a result, pigeons are an odd choice of subject if investigators are interested in showing that satiety factors contribute to within-session decreases in operant responding.

PROBLEMS WITH SENSITIZATION-HABITUATION

Although sensitization-habituation has advantages over arousal-satiation as an explanation for the within-session changes in op-

erant responding, it also has some flaws. To begin with, the hypothesis has mechanisms that both increase (e.g., sensitization) and decrease (habituation) response rate. Postulating two factors gives a theory a lot of latitude. However, postulating two factors may be necessary to explain the frequently bitonic within-session changes in responding. In addition, research on sensitization-habituation constrains the conditions under which response rates may increase. Increases may occur when only a few stimuli have been presented (sensitization); after the presentation of a strong, different, or extra stimulus (dishabituation); after a change in the nature of the stimulus (violations of stimulus specificity); or when the stimulus has not been presented for a time (spontaneous recovery). If increases occur under other conditions or fail to occur under these conditions, then the theory is wrong or at least incomplete.

The sensitization-habituation model is also an empirical generalization rather than a formal theory. It states only that whatever produces sensitization and habituation to stimuli, such as lights and tones, also produces the dynamic changes in reinforcer effectiveness that occur within a session. It leaves those processes unidentified. An empirical approach is necessary at present because the leading models of habituation (e.g., Sokolov, 1963; Wagner, 1976) have been severely criticized (e.g., Mackintosh, 1987; Staddon & Higa, 1996). An empirical approach also has an important advantage: Theory-based research becomes less useful when the theory on which it is based is questioned. Nevertheless, our hypothesis would have more content if a generally accepted theory of habituation were available.

Many questions have not yet been answered about sensitization and habituation. For example, rate of operant responding may decrease within the session for one subject, but response rate first increases and then decreases for another subject. Similar individual differences in rates of sensitization and habituation are frequently reported (e.g., Hinde, 1970). However, the factors that determine why sensitization or habituation is stronger for one subject than for another remain to be identified.

Finally, the sensitization-habituation explanation may be incomplete. For example, satiety factors other than habituation may eventually be shown to play a role in regulating the within-session changes in conditioned responding. At present, however, the only variables that have been shown to play a role remain sensitization and habituation. Table 2 shows that the role of these variables is well supported. In contrast, the arguments for other satiety variables are limited and ambiguous. In addition, some of the evidence presented in Table 2 suggests that the contribution of habituation is large enough to overcome the contribution of other satiety factors. Therefore, other satiety variables may play a smaller role in producing within-session changes in responding than intuition might initially suggest.

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ERRATUM

Kennedy, C. H., Meyer, K. A., Werts, M. G., & Cushing, L. R. (2000). Effects of sleep deprivation on free-operant avoidance. *Journal of the Experimental Analysis of Behavior, 73,* 333–345.

Error: Citation of the effects of sleep deprivation in Kennedy and Itkonen (1993) and Iwata (1994). Correction: Neither article refers to sleep deprivation.