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HABITUATION CONTRIBUTES TO WITHIN-SESSION CHANGES IN FREE WHEEL RUNNING

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Three experiments tested the hypothesis that habituation contributes to the regulation of wheel running. Rats ran in a wheel for 30-min sessions. Experiment 1 demonstrated spontaneous recovery. Rats ran more and the within-session decreases in running were smaller after 2 days of wheel deprivation than after 1 day. Experiment 2 demonstrated dishabituation. Running rate increased immediately after the termination of a brief extra event (application of the brake or flashing of the houselight). Experiment 3 demonstrated stimulus specificity. Rats completed the second half of the session in either the same wheel as the first half, or a different wheel. Second-half running was faster in the latter case. Within-session patterns of running were well described by equations that describe data from the habituation, motivation, and operant literatures. These results suggest that habituation contributes to the regulation of running. In fact, habituation provides a better explanation for the termination of wheel running than fatigue, the variable to which this termination is usually attributed. Overall, the present findings are consistent with the proposition that habituation and sensitization contribute to the regulation of several forms of motivated behavior.

Key words: within-session changes in responding, habituation, spontaneous recovery, dishabituation, stimulus specificity, wheel running, rats

The term *motivation* usually applies to behavior that is energetic and goal directed. Types of behavior such as feeding, drinking, aggression, exploration, escape, curiosity, and drug taking usually fall under this heading. A salient characteristic of motivated behavior is that it occurs in bouts (see, e.g., Richter, 1927). Early theories of motivation explained these bouts in terms of a general process such as homeostasis, hedonism, instincts, drives, or incentives. The general process approach to motivation was abandoned as each of these theories encountered problems.

Recently, McSweeney and Swindell (1999) proposed a new general process theory of motivation. They argued that two simple assumptions might contribute to understanding a variety of motivated behavior. First, the goal objects (e.g., food or water) of motivated behavior serve as reinforcers. Second, animals sensitize and then habituate to reinforcers (i.e., goal objects) with repeated contact, thereby altering the capacity of these goal objects to control behavior. Sensitization is an increase in responsiveness to a stimulus that often occurs with the initial presentation of the stimulus. Habituation is a decrease in responsiveness that develops with later stimulus presentations (see, e.g., Groves & Thompson, 1970). As animals habituate to a goal object, the goal object loses its effectiveness, and the behavior directed toward that goal stops. Unlike past general process theories, McSweeney and Swindell's account views habituation (and its accompanying process, sensitization) as only one among many contributors to the regulation of motivated behavior.

McSweeney and Swindell (1999) showed that, consistent with this idea, the empirical characteristics of motivated behavior are similar to the empirical characteristics of behavior undergoing sensitization and habituation. Motivated behavior decreases in strength through contact with the goal (habituation) and increases in strength in the absence of the goal (spontaneous recovery). Such behavior may increase in strength with initial contact with the goal (sensitization precedes habituation), with the presentation of irrelevant stimuli (sensitization), with changes in the goal object (stimulus specificity), and with the presentation of dishabituators (dishabituation). Finally, an equation that describes data from the habituation literature accounts for approximately 90% of the vari-

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ance in the temporal changes in several forms of motivated behavior (feeding, drinking, exploration, and escape).

The purpose of the present study was to test the sensitization-habituation theory for wheel running. Wheel running was chosen for study because its termination is usually attributed to fatigue (e.g., Belke, 1997) rather than to habituation. Many other studies have already shown that habituation may contribute to the termination of feeding and drinking (e.g., Swithers & Hall, 1994). Termination of such behavior usually is attributed to satiation. Showing that habituation can provide a simple unifying explanation for behavior that usually is attributed to different explanatory variables would help to simplify the description of motivated behavior.

Wheel running is motivated behavior for rats because it is energetic and goal directed. Rats run upwards of 5 km per night (Eikelboom & Mills, 1988; Looy & Eikelboom, 1989; Richter, 1927). Wheel running also serves as a reinforcer. That is, rats lever press to gain access to a wheel (e.g., Belke, 1997, 1998, 2000a, 2000b; Belke & Heyman, 1994; Collier & Hirsch, 1971; Iversen, 1993; Pierce, Epling, & Boer, 1986), and Herrnstein's (1970) response-strength equation describes rats' responding reinforced by the opportunity to run (Belke, 1998; Belke & Heyman, 1994). Nevertheless, only a few published reports have described within-session patterns of wheel running (for free running, see Skinner, 1933; for operant behavior reinforced by opportunity to run, see Belke, 1997, 2000a; for wheel running reinforced by food, see Weatherly, McMurry, & Melville, 1999). Therefore, the sensitization-habituation theory of wheel running invites further tests.

In this study, three experiments examined whether free wheel running showed three of the fundamental empirical characteristics of behavior undergoing habituation. Experiment 1 examined whether spontaneous recovery would occur. Experiment 2 examined whether wheel running could be dishabituated. Experiment 3 examined whether stimulus specificity would occur. Finally, equations that have been applied to data from the habituation literature and to several forms of motivated behavior also were applied to wheel running.

EXPERIMENT 1

Spontaneous recovery, the recovery of responsiveness to a habituated stimulus when that stimulus is not presented, is a fundamental property of habituated behavior (see, e.g., Thompson & Spencer, 1966).[1] If habituation contributes to the regulation of motivated behavior, then spontaneous recovery should occur for that behavior. The spontaneous recovery of habituated behavior usually increases with length of stimulus withdrawal (e.g., Hinde, 1970). Consistent with this characteristic of habituation, the rate of wheel running increases with degree of wheel deprivation, up to 46.5 hr (e.g., Hill, 1956; Mueller, Herman, & Eikelboom, 1999). The present study attempted to replicate this increase in the size of spontaneous recovery over time, and to examine within-session patterns of wheel running to provide a more complete test of the sensitization-habituation theory of wheel running.

Method

Subjects. The subjects were 8 experimentally naive male rats bred from Sprague-Dawley stock at Washington State University. They were approximately 140 days old at the start of the experiment. All subjects were maintained at approximately 80% of their free-feeding body weights by postsession feedings. The 80% body weights ranged from 325 to 368 g. Subjects were housed individually and were maintained on a 12:12 hr light/dark cycle.

Apparatus. Four identical stainless steel wire-mesh wheels were used. The diameter and width of the activity wheels were 35.5 cm and 10.0 cm, respectively. The force required to turn the wheel was approximately 0.065 N.

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[1] Notice that the definition of *spontaneous recovery* in the habituation literature is slightly different from the definition of *spontaneous recovery* in the conditioning literature. In the conditioning literature, spontaneous recovery refers to the recovery of extinguished conditioned responding after a period of time. In the habituation literature, spontaneous recovery refers to the recovery of responding to a habituated stimulus after a period of time in the absence of that stimulus. In both cases, spontaneous recovery refers to a loss of a learned behavior change as a result of the absence of the precipitating events. For a discussion of the relation between the spontaneous recovery of habituated behavior and the spontaneous recovery of extinguished behavior, see McSweeney, Swindell, and Weatherly (1999).

Each wheel was housed in a sound-attenuating shell, equipped with a fan for ventilation and to mask extraneous noise. A solenoid-operated brake was attached to each wheel. When the solenoid was operated, a metal hook contacted the outer wire-mesh floor of the wheel, causing the wheel to stop abruptly. A microswitch attached to the wheel frame recorded revolutions. A houselight (24-VDC) mounted on the side of the wheel frame illuminated the inside of the wheel chamber. Experimental events were presented and data were recorded by an IBM-compatible computer connected to the wheel via a MED Associates interface. The number of wheel revolutions was recorded in 1-min bins.

Procedure. Each rat was placed in a running wheel for 30 min each day over a 20-day training period. When the rat was placed in the wheel, the brake was applied and the houselight was off. After 1 min had elapsed, the brake was released and the houselight was illuminated for 30 min. Then the brake was applied and the light went off. After the first 10 days, 2 rats (S102 and S103) were eliminated from the experiment because their wheel running was slow (fewer than 10 revolutions per 30 min). No data are presented for these rats. Eliminating rats that show little running is a common practice in the wheel-running literature (e.g., Belke & Heyman, 1994).

After the last day of training, the rats were tested under two levels of wheel deprivation. One condition was 1-day deprivation, in which subjects spent 23.5 hr in their home cages before the experimental sessions. The other condition was 2-day deprivation, in which subjects spent 47.5 hr in their home cages before the experimental sessions. Wheel-deprivation levels alternated every experimental session. Every rat received 16 sessions, consisting of eight 1-day and eight 2-day wheel-deprivation sessions. Preliminary research showed that rats' running became stable according to visual inspection within this period. Sessions always occurred during the last half of the light phase of the daily cycle. Holding the time of testing constant was important because wheel running shows a strong circadian rhythm (e.g., Eikelboom & Mills, 1988).

Results and Discussion

Results represent the last five sessions of the 1-day and 2-day wheel-deprivation conditions. Figure 1 presents the mean response rate during successive 3-min blocks for each rat. Within-session patterns of wheel running were stable, as indicated by the small error bars. Every rat showed a within-session decrease in response rate.

All rats showed higher overall running rates after the 2-day wheel-deprivation condition. This result is consistent with previous research on wheel running (e.g., Hill, 1956; Mueller et al., 1999). In addition, all rats ran at higher rates during the early part of the sessions than during the later part of the sessions. Thus, consistent with previous research in the habituation literature (e.g., Hinde, 1970), spontaneous recovery occurred in the form of an increase in responding from the end of one session to the beginning of the next session.

Every rat except S105 showed a similar initial response rate and a steeper within-session decrease under the 1-day deprivation condition than under the 2-day condition. A two-way (Deprivation × Time Interval) repeated measures analysis of variance (ANOVA) was applied to the rates of running by individual subjects during successive 3-min intervals in the session. The main effect of time was significant, $F(9, 45) = 15.71$, $p < .01$, indicating that rate of running changed within sessions. The main effect of deprivation was also significant, $F(1, 5) = 16.14$, $p < .01$, indicating that wheel running was faster under the condition of greater deprivation. Further, the interaction between deprivation and time was significant, $F(9, 45) = 2.12$, $p < .05$, indicating that the patterns of responding within sessions differed between the 1-day and 2-day deprivations.

In summary, spontaneous recovery was evident in two ways that are consistent with the findings of previous studies (e.g., Hill, 1956; Mueller et al., 1999). That is, the more the rats were deprived of wheel running, the more they ran in the wheel. In addition, wheel running increased from the end of one session to the beginning of the next session. These results are consistent with the hypothesis that habituation contributes to the regulation of wheel running. However, fatigue

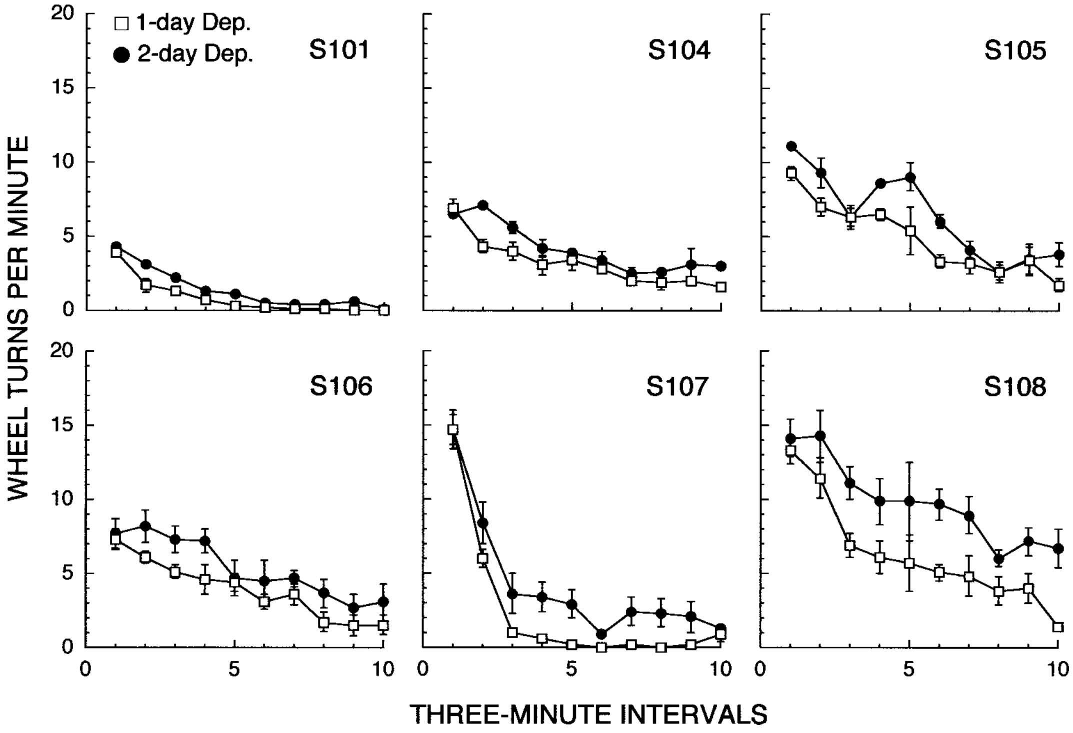

Fig. 1. Experiment 1: response rate (number of wheel turns per minute) during successive 3-min intervals in the session for each wheel deprivation condition (1 day vs. 2 days) for each rat. Error bars indicate standard errors of the means. When error bars are not apparent, the bars were smaller than the diameter of the data symbols.

also provides an alternative, intuitively appealing, explanation for the results. Recovery from fatigue should be greater for animals deprived of exercise for a longer period. In the past, researchers have distinguished between habituation and fatigue by demonstrating dishabituation (e.g., Smotherman & Robinson, 1992) and stimulus specificity (e.g., Swithers & Hall, 1994). This was attempted in Experiments 2 and 3.

EXPERIMENT 2

Dishabituation, a fundamental property of habituated behavior, is defined as the increase in responding to a stimulus following the presentation of a strong, different, or extra stimulus (see, e.g., Groves & Thompson, 1970). To our knowledge, the prediction that dishabituation will occur for motivated behavior is unique to the sensitization-habituation theory. Therefore, evidence supporting this prediction would provide strong support for the idea that sensitization-habituation contributes to the control of motivated behavior. For example, there is no reason to expect a dishabituating event to reduce fatigue.

In this experiment, baseline sessions consisted of 30 min of free running. Dishabituation sessions were similar except that dishabituating stimuli were also presented. Habituation theory predicts that subjects would run more after the termination of the dishabituating stimuli than during the corresponding time in the baseline sessions.

Method

The same rats and apparatus were used as in Experiment 1. Experimental sessions occurred 5 days per week (Monday through Friday). Because the Monday session followed a 3-day wheel-deprivation period, it was treated as an adjustment session and the subject always experienced 30 min of free running. Baseline and dishabituation sessions alternated during the remainder of the week. The experiment was conducted in two phases, each of which lasted for eight baseline and eight dishabituation sessions distributed over 4 weeks. Baseline sessions were 30 min of free

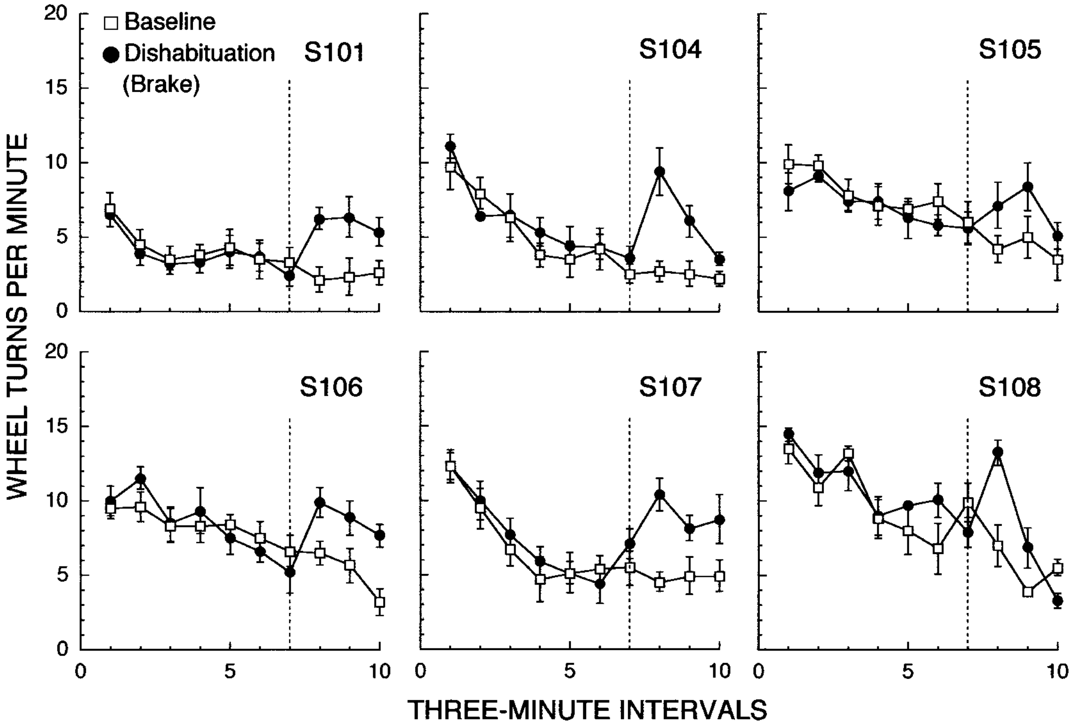

Fig. 2. Experiment 2: response rate (number of wheel turns per minute) during successive 3-min intervals in the session for each condition (dishabituation vs. baseline) under the brake test for each rat. Error bars indicate standard errors of the means. When error bars are not apparent, the bars were smaller than the diameter of the data symbols. Vertical dashed lines indicate the seventh block, in which the dishabituating event occurred in the dishabituation sessions.

running, as in Experiment 1. During the dishabituation sessions, the first 20 min and 55 s were free running, followed by a 5-s dishabituating event. The last 9 min were free running.

A different dishabituating event was presented in each of the two phases. In the first test phase (brake test), the brake was applied for 1 s, released for 1 s, and so on, for a total of 5 s. The rat did not run during this time. In addition, the rat could hear the sound of brake operating. In the second test phase (light test), the houselight went off for 1 s, on for 1 s, and so on, for a total of 5 s. The rat could run during this dishabituating event, because the brake was not applied. Other aspects of the experiment remained the same as for baseline sessions.

Results and Discussion

Results were taken from the last five of each of the baseline and dishabituation sessions. Figures 2 and 3 present results from the brake and light tests, respectively. They present the response rate during successive 3-min blocks for each rat. Within-session patterns of wheel running were stable, as indicated by the small error bars. Results from the two tests were similar. During the first six 3-min blocks, running did not differ in the baseline and dishabituation sessions. After the seventh block, all rats ran more in the dishabituation sessions than in the baseline sessions. In other words, the extra events increased response rate, demonstrating dishabituation. The effects of the dishabituating manipulations were temporary. Response rates rapidly decreased once the dishabituating events ended. This rapid decay of dishabituated responding is consistent with past studies of habituation (e.g., Groves & Thompson, 1970).

A two-way (Condition × Time Interval) repeated measures ANOVA was applied to the results in each figure. The main effects of time were significant—for the brake test, *F*(9,

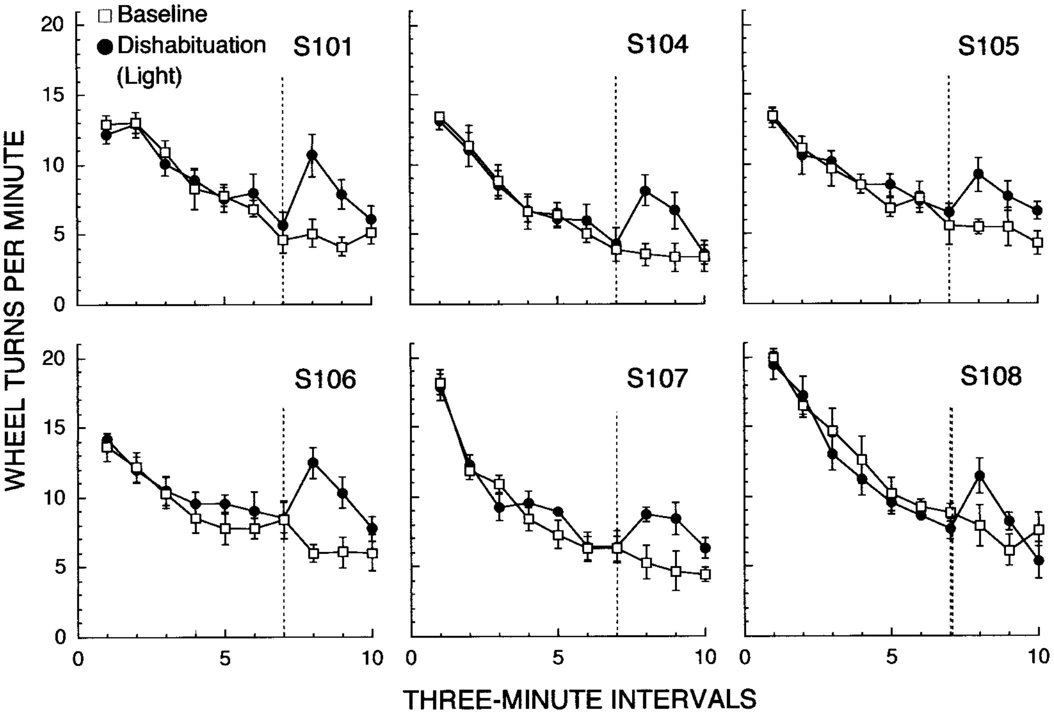

Fig. 3. Experiment 2: response rate (number of wheel turns per minute) during successive 3-min intervals in the session for each condition (dishabituation vs. baseline) under the light test for each rat. Error bars indicate standard errors of the means. When error bars are not apparent, the bars were smaller than the diameter of the data symbols. Vertical dashed lines indicate the seventh block, in which the dishabituating event occurred in the dishabituation sessions.

45) = 11.61, $p < .01$; for the light test, $F(9, 45) = 51.71$, $p < .01$—indicating that responding changed within sessions. The main effects of condition (baseline vs. dishabituation) were also significant—for the brake test, $F(1, 5) = 29.03$, $p < .01$; for the light test, $F(1, 5) = 13.48$, $p < .05$—indicating that the dishabituating events altered response rates. Furthermore, the interactions between condition and time were significant—for the brake test, $F(9, 45) = 10.65$, $p < .01$; for the light test, $F(9, 45) = 25.43$, $p < .01$. For the brake test, analyses of simple effects revealed significant differences between baseline and dishabituation sessions in the last three 3-min blocks but not in the first seven 3-min blocks. For the light test, significant differences were observed only in the eighth and ninth 3-min blocks.

The present results are inconsistent with fatigue as an explanation for within-session decreases in wheel running. There is no obvious reason why applying a brake or flashing a houselight for 5 s should substantially alter fatigue. In addition, individual subjects sometimes ran more during the seventh block (which contained the dishabituating events) in the dishabituation sessions than in the baseline sessions (see Figures 2 and 3). More running during the seventh block should have produced more fatigue. Therefore, if fatigue contributes to the regulation of wheel running, those rats should show less running during the last 9 min of the dishabituation sessions than during baseline sessions. Nevertheless, all rats ran more after the removal of the dishabituating event than during the corresponding period of baseline sessions.

The increases in running after the dishabituating events might be attributed to surprise or fear of the dishabituating stimuli. In rats, however, surprise or fear usually decreases rather than increases response rate. For example, rats often freeze in the presence of feared stimuli (e.g., Bolles & Collier, 1976). Exploratory behavior also is suppressed, not facilitated, by fear (e.g., Montgomery & Monkman, 1955). It seems likely, therefore, that surprise or fear caused by the novel stimulus should have decreased rates of wheel running during the terminal intervals of the dishabituation sessions.

Dishabituation, therefore, remains the most likely explanation for terminal-interval changes in wheel running in Experiment 2. This outcome is consistent with the sensitization-habituation theory of McSweeney and Swindell (1999), and apparently is not predicted by competing theories.

EXPERIMENT 3

Habituation is relatively specific to the stimulus that is presented (stimulus specificity; see, e.g., Hinde, 1970; Swithers & Hall, 1994). Therefore, discriminable changes in the stimulus reduce habituation. A demonstration of stimulus specificity would question fatigue as an explanation for the decrease in responding. Changes in the stimulus should not restore responding if the subject is fatigued. To our knowledge, stimulus specificity has not been shown for wheel running.

In this experiment, two different wheels were used. In every session, rats were exposed to two consecutive 15-min running periods. In the baseline condition, rats were exposed to the same wheel for the first and second running periods. In the experimental condition, rats were exposed to different wheels for the first and second running periods. If habituation contributes to the within-session decreases in wheel running, rats should run faster during the second 15-min running period in the experimental condition than in the baseline condition. That is, changing the wheel should reduce habituation and increase response rates.

Method

Subjects. The same rats were used as in previous experiments.

Apparatus. Two activity wheels were used. One was the same wire-mesh wheel used in the previous experiments. The other was identical except that its entire floor was covered with gray tape. Thus, the wheels likely differed in their visual, olfactory, and tactile properties. Covering the floor with visual-tactile stimuli is often used as the discriminative stimulus in maze experiments (e.g., Jarrard, Okaichi, Steward, & Goldschmidt, 1984). Other aspects of the apparatus were identical to Experiments 1 and 2.

Table 1

Mean number of wheel turns and the standard error of the mean during the 30-min adaptation sessions for original and covered wheels for each rat in Experiment 3. Data are averages from the four sessions in each condition.

		Rat					
		S101	S104	S105	S106	S107	S108
Original	*M*	140.8	52.0	93.5	111.5	91.5	251.8
	SE	10.5	7.1	7.8	12.3	10.8	13.8
Covered	*M*	44.0	48.8	42.3	78.3	73.5	215.3
	SE	8.4	7.8	2.3	7.6	6.6	11.4

Procedure. The first 8 days were 30-min adaptation sessions. For each rat, the two wheels were alternated across days. Because 2 rats (S101 and S105) ran much more in the wire-mesh wheel than in the tape-covered wheel, they were eliminated from the experiment after the initial sessions. The remaining 4 rats also ran more in the original wheel than the covered wheel, but the differences were smaller (see Table 1).

After this period, the rats were tested under two conditions: experimental (original-covered) and baseline (covered-covered). The two conditions alternated across days. After 4 days of these sessions, the experiment was discontinued for approximately 2 months due to a malfunction of the apparatus that recorded number of wheel turns. During this period, the rats were given 30-min access to each wheel 2 days per week, but responses could not be recorded. Thereafter, the experiment resumed for 16 days, and consisted of eight baseline and eight experimental sessions.

In both conditions, a session consisted of two 15-min free running periods. For the original-covered condition, the rat was placed in the original wire-mesh wheel during the first 15-min running period and then in the covered wheel during the second 15-min period. For the covered-covered condition, the subject was placed in the same covered wheel during the first and second 15-min running periods. Between the first and the second periods, the brake was applied and the houselight was off for 1 min, during which time the rat was removed from the wheel and held by the experimenter. Other aspects of the pro-

Table 2

Mean number of wheel turns and the standard error of the mean during the first and second 15-min running periods for each rat in the original-covered and covered-covered conditions. Data are averages from the last four sessions in each condition.

		First 15-min period		Second 15-min period	
Rat		Original-covered	Covered-covered	Original-covered	Covered-covered
S104	*M*	41.8	32.5	31.0	22.8
	SE	2.6	1.8	2.9	2.0
S106	*M*	86.0	93.3	83.3	75.0
	SE	6.8	4.4	8.6	11.5
S107	*M*	74.3	61.5	71.5	52.0
	SE	7.0	7.0	7.1	4.6
S108	*M*	213.0	196.3	154.3	124.8
	SE	17.1	13.0	18.4	14.5
M		103.8	95.9	85.0	68.6

cedure were the same as in previous experiments.

The wire-mesh wheel was used during the first 15-min running period in the experimental condition to distinguish habituation from fatigue. Because rats usually ran more in the original than the covered wheel (Table 1), they should be more fatigued at the beginning of the second 15-min period in the original-covered condition than in the covered-covered condition. Therefore, if fatigue contributes to the regulation of wheel running, rats should run less during the second 15-min period of the original-covered condition. This prediction is opposite to that of habituation theory, which predicts that rats should run more during the second 15-min period of the original-covered condition, because stimulus conditions change in that condition.

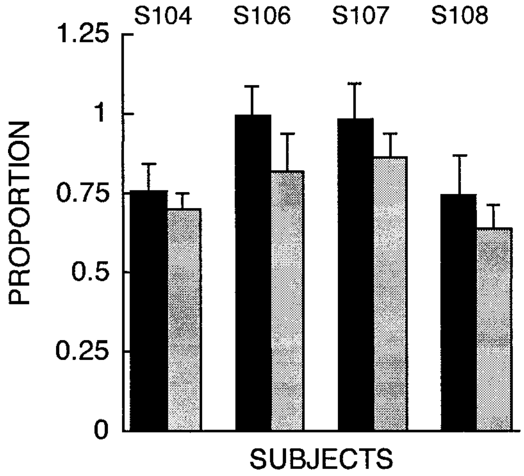

Fig. 4. Experiment 3: number of wheel turns in the second 15-min running period as a proportion of number of wheel turns during the first 15-min running period for the original-covered and covered-covered conditions for each rat. Proportions were calculated for each session for each subject and then averaged over the last four sessions. Black bars indicate the original-covered condition, and gray bars indicate the covered-covered condition. Error bars indicate standard errors of the means.

Results and Discussion

Within-session patterns are not presented because those patterns were variable from subject to subject and their standard errors were larger than those for the patterns reported in Figures 1 to 3. By aggregating the data across 3-min blocks, however, it is still possible to examine the prediction of stimulus specificity that rats should run faster during the second half of the session in the original-covered (stimulus changed) condition than in the covered-covered (stimulus constant) condition.

Table 1 shows the mean number of wheel turns averaged over the four 30-min adaptation sessions for the original and the covered wheels. All rats ran more in the original wheel than in the covered wheel, and the differences were often large. These results show that the rats discriminated the wheels.

Table 2 shows the mean number of wheel turns during the first and second 15-min periods for the original-covered and covered-covered conditions during the last four sessions of each. Number of wheel turns was stable, as indicated by the small standard errors. During the first 15-min running period, every rat except S106 ran faster in the original-covered condition than in the covered-covered condition. In other words, 3 of 4 rats ran faster in the original wheel than in the covered wheel. This difference was not statistically significant, $t(3) = 1.49$, *ns.*

Table 2 confirms the prediction of stimulus specificity. That is, running in the covered wheel during the second 15-min period was faster when the rats had run in the different (original) wheel than in the same (covered) wheel during the first 15-min period. This difference was statistically significant when assessed by a paired *t* test, $t(3) = 3.20$, $p < .05$.

Figure 4 summarizes the results shown in

Table 2. It presents number of wheel turns in the second 15-min period as a proportion of number of wheel turns in the first 15-min period for each rat in both conditions. Figure 4 confirms the prediction from the habituation hypothesis, because second-half responding was faster relative to first-half responding in the original-covered condition than in the covered-covered condition for all rats.

Although the present results are consistent with the predictions of stimulus specificity, they are not uniquely predicted by that hypothesis. Rats also might have run faster during the second half of the original-covered condition as a result of momentum that carried over from the first to the second half of the session (see, e.g., Nevin, Mandell, & Atak, 1983). The data are consistent with this interpretation as well as with the stimulus-specificity hypothesis.

The present results are not consistent with fatigue. Because 3 of 4 rats ran more during the first half of the session in the original-covered condition, the rats should have been more fatigued at the beginning of the second half of the session in the original-covered condition. Therefore, these rats should have run less during the second half of the session in the original-covered condition. As Figure 4 shows, just the opposite occurred.

APPLICATION OF QUANTITATIVE MODELS

The three experiments showed that wheel running has empirical characteristics similar to those of behavior undergoing habituation. This suggests that sensitization-habituation may contribute to the regulation of wheel running. To further explore the parallel between wheel running and habituated behavior, a quantitative model of within-session changes resulting from sensitization and habituation (McSweeney & Swindell, 1999) was applied to the present data:

$$P = \frac{b}{e^{aT}} - \frac{c}{c + T}. \qquad (1)$$

P is the predicted proportion of the total responses that should occur during successive time intervals (T). T is the ordinal number of time interval, e is the base of the natural logarithm, and a, b, and c are free parameters. The exponential part of Equation 1 describes a decreasing process identified as habituation; the hyperbolic part describes an increasing process identified as sensitization. Thus, a and b govern habituation, and c applies to sensitization. Larger values of a and b mean larger late-session decreases in responding (i.e., greater habituation), and larger values of c mean larger early-session increases in responding (i.e., greater sensitization). Equation 1 has described within-session data from habituation (McSweeney, Hinson, & Cannon, 1996) and motivation (McSweeney & Swindell, 1999) experiments well, accounting for approximately 90% of the variance in the data. If habituation contributes to the regulation of wheel running, Equation 1 should also describe within-session patterns of wheel running.

It was possible to reduce the number of free parameters because few within-session increases in running (sensitization, c) were observed. As a result, a simplified model,

$$P = \frac{b}{e^{aT}}, \qquad (2)$$

was applied to the proportion of total-session responses during successive 3-min blocks in the session for individual subjects and for the mean of all subjects in Experiment 1 and in the baseline conditions of Experiment 2. Equation 2 was not applied to the dishabituation conditions of Experiment 2 and to Experiment 3 because the stimulus changes introduced in those experiments should disrupt habituation. Results for the mean were calculated by dividing the number of revolutions per 3-min block by the number of total revolutions in the session for the mean of all subjects. That is, P is the proportion calculated for the mean of all subjects, not the mean of the proportions for individual subjects. Table 3 contains the parameters and fit of Equation 2 for individual subjects and for the mean of all subjects.

Equation 2 usually described well the proportion of total-session responses during successive 3-min intervals in the session, as indicated by the percentage of the variance accounted for (r^2), which was greater than 94% for all fits to group mean data and greater than 80% for 16 of 22 individual-subject fits. In Experiment 1, a and b were both larger for 1-day deprivations than for 2-day dep-

Table 3

Parameters *a* and *b* and the percentage of the variance accounted for (r^2) when Equation 2 was fitted to the proportion of total-session responses during successive 3-min intervals in the session.

	Experiment 1						Experiment 2					
	1-day deprivation			2-day deprivation			Baseline (brake)			Baseline (light)		
Rat	*a*	*b*	r^2	*a*	*b*	r^2	*a*	*b*	r^2	*a*	*b*	r^2
S101				.336	0.400	90.4	.100	0.164	76.8	.133	0.192	90.3
S104	.144	0.200	92.3	.112	0.173	80.4	.162	0.214	88.9	.160	0.220	95.3
S105	.165	0.220	90.2	.147	0.201	75.0	.107	0.171	88.7	.117	0.180	95.3
S106	.185	0.240	92.3	.126	0.187	90.1	.094	0.161	76.4	.091	0.159	89.8
S107				.220	0.240	66.4	.086	0.152	62.3	.145	0.201	94.2
S108	.189	0.242	85.8	.090	0.158	88.4	.111	0.172	73.4	.121	0.182	93.3
M	.198	0.249	95.2	.136	0.195	94.9	.107	0.171	96.1	.126	0.187	96.5

Note. Equation 2 cannot be applied to S101 and S107 during the 1-day deprivation condition because no responding was observed in some 3-min intervals. Exponential functions cannot be applied to data when they contain 0. Parameters in the row indicated *M* show the parameters of Equation 2 when it was applied to the proportion of total-session responses calculated for the mean of all rats. Thus, the parameters in this row are not the mean of parameters for individual rats.

rivations, both for the mean of all subjects and for all individuals for which comparisons could be made. This suggests that habituation to the wheel occurred faster and was more pronounced after 1 day than after 2 days of wheel deprivation.

Aoyama and McSweeney (2001) pointed out that when the rate of consummatory behavior (R_r) is described as an exponential function of time, the rate of consummatory behavior must be described as a linear function of cumulative amount of consumption (R_c). Equation 3 is a linear equation that is mathematically equivalent to Equation 2 for consummatory behavior or operant behavior under ratio schedules:

$$R_r = b - aR_{c,} \qquad (3)$$

where R_r is response rate. For consummatory behavior, R_r is the same as the obtained rate of reinforcement, because each response results in some consumption. R_c is cumulative number of reinforcers (i.e., total amount consumed); *a* and *b* are free parameters. Parameter *b* is the *y*-axis intercept of the regression line (i.e., response rate at the beginning of the session), and *a* is the slope of the regression line (i.e., the decrease in response rate produced by an obtained reinforcer).

Running is consummatory behavior, and revolutions can be considered a unit of consumption (Belke & Heyman, 1994). Accord-

Table 4

Parameters *a* and *b* and the percentage of the variance accounted for (r^2) when Equation 3 was fitted to response rats during successive 3-min intervals in the session.

	Experiment 1						Experiment 2 (brake)					
	1-day deprivation			2-day deprivation			Baseline			Dishabituation (1–6)		
Rat	*a*	*b*	r^2	*a*	*b*	r^2	*a*	*b*	r^2	*a*	*b*	r^2
S101	.156	3.81	99.1	.100	4.30	99.0	.036	5.78	78.5	.039	5.42	61.9
S104	.051	6.03	91.4	.017	6.93	87.9	.060	9.32	94.0	.059	9.85	88.3
S105	.049	9.03	94.0	.016	10.98	80.5	.032	10.17	91.2	.024	8.81	77.4
S106	.050	7.34	95.5	.017	8.66	90.6	.025	10.21	84.2	.033	11.21	80.7
S107	.216	14.90	99.1	.072	13.19	90.5	.039	10.31	73.7	.066	12.29	99.4
S108	.058	12.75	93.6	.019	14.29	91.6	.034	13.50	78.4	.028	13.71	76.6
M	.072	8.30	95.3	.047	9.35	96.7	.035	9.78	96.2	.039	10.11	97.5

Note. Parameters in the row indicated *M* show the parameters of Equation 3 when it was applied to the mean response rates of all subjects. Thus, the parameters in the row are not the mean of parameters for individual subjects.

ingly, if habituation contributes to wheel running, within-session decreases in wheel running should be described as a linear function of cumulative number of wheel turns. Equation 3 was applied to the mean response rates for all subjects during successive 3-min blocks during Experiment 1. The values of *a* and *b* and the percentage of the variance accounted for (r^2) by Equation 3 are shown in Table 4. The fit of the equation to the group mean data is also illustrated in Figure 5. Table 4 and Figure 5 show that response rates were well described as linear functions of the cumulative number of wheel turns in Experiment 1. The equation always accounted for at least 80% of the variance in the data. The *y*-axis intercept (*b*) was usually smaller and the slope (*a*) was always steeper in the 1-day deprivation condition. As a result, the *x*-axis intercept was smaller in the 1-day deprivation condition, and the difference in the *y*-axis intercept remained small (Figure 5). The small difference in the *y*-axis intercepts means that running should be slightly faster at the beginning of the session under the 1-day deprivation than under the 2-day deprivation. The difference in the slopes means that one wheel turn lessens the running speed more under the 1-day deprivation than under the 2-day deprivation. The *x*-axis intercept theoretically predicts the cumulative number of wheel turns that will reduce running speed to zero. Thus, rats would run more in a running episode when they have been deprived of running for longer periods.

Table 4 and Figure 5 also present results for the dishabituating brake and light conditions. Three regression lines were calculated for each test condition (baseline sessions, Blocks 1 through 6 of dishabituation sessions, and Blocks 8 through 10 of dishabituation sessions). The fit of the equation was usually good for the baseline and light dishabituation sessions, although confidence in this outcome is tempered by the few data points available for analysis. A few poorer fits occurred for individual subjects during the brake dishabituation sessions. In general, the regression lines for the baseline and for the first six 3-min blocks of the dishabituation sessions were similar. In contrast, the regression lines for the last three 3-min blocks of the dishabituation sessions usually had larger *y*-axis intercepts and steeper slopes than the regression lines for baseline sessions. In other words, the dishabituation manipulations altered the *y*-axis intercepts and the slopes but not the *x*-axis intercepts of the regression lines (see Figure 5).

GENERAL DISCUSSION

This study examined wheel running to test the sensitization-habituation hypothesis for the regulation of motivated behavior (McSweeney & Swindell, 1999). It asked whether wheel running would show three of the fundamental characteristics of behavior undergoing habituation: spontaneous recovery, dishabituation, and stimulus specificity. Experiment 1 showed that rats ran faster when they were deprived of wheel running for 2 days rather than 1 day (spontaneous recovery). Experiment 2 showed that subjects

Table 4

(*Extended*)

Experiment 2 (brake)			Experiment 2 (light)								
Dishabituation (8–10)			Baseline			Dishabituation (1–6)			Dishabituation (8–10)		
a	*b*	r^2	*a*	*b*	r^2	*a*	*b*	r^2	*a*	*b*	r^2
.023	8.27	61.9	.044	13.69	95.0	.035	12.86	87.7	.083	26.84	99.9
.126	25.18	99.8	.057	13.22	98.2	.057	12.99	97.2	.102	25.53	93.2
.045	14.69	41.5	.039	12.82	96.7	.036	12.73	94.4	.052	19.20	99.7
.040	17.03	99.6	.032	12.97	92.1	.030	13.48	90.3	.069	27.72	98.8
.032	15.05	57.4	.054	16.06	93.7	.059	16.50	90.3	.048	19.17	84.1
.164	50.19	99.9	.042	19.17	97.0	.045	19.57	98.6	.102	38.17	99.7
.074	20.76	99.8	.044	14.60	97.9	.045	14.65	97.8	.076	25.98	98.9

ran faster after a dishabituating event had ended than during the corresponding period of baseline sessions (dishabituation). Experiment 3 showed that running was faster during the second half of a session following a switch in wheels than following no switch (stimulus specificity). Finally, quantitative models that successfully describe behavior undergoing sensitization and habituation also described within-session patterns of wheel running. These results suggest that habituation contributes to the control of wheel running, insofar as conformity to the empirical characteristics of habituation is regarded as a test for its presence (e.g., Leaton & Tighe, 1976; Teyler, Chiaia, DiScenna, & Roemer, 1984).

Arguing that habituation helps to regulate wheel running does not preclude the possibility that other variables may also contribute. In fact, other theories are compatible with some parts of the present data. For example, the results of Experiment 3 (stimulus specificity) may be as compatible with momentum theory as they are with habituation theory. The results of Experiment 1 (spontaneous recovery) are compatible with recovery from fatigue. Only habituation theory, however, provides a parsimonious explanation for all of the data presented here.

Habituation theory is also compatible with some past results that have argued for a role of fatigue in terminating wheel running. For example, Skinner (1933) and Collier, Hirsch, Levitsky, and Leshner (1975) showed that running decreased as the force required to turn the wheel increased. Changing response force should alter rate of habituation because changing the nature of the response usually alters the rate of habituation (e.g., Hinde, 1970). Therefore, habituation provides an explanation for even these data.

Skinner (1933) reported within-session decreases in free wheel running similar to those in the present study. In contrast, Belke (1997, 2000a) investigated the within-session pattern of operant responding reinforced by the op-

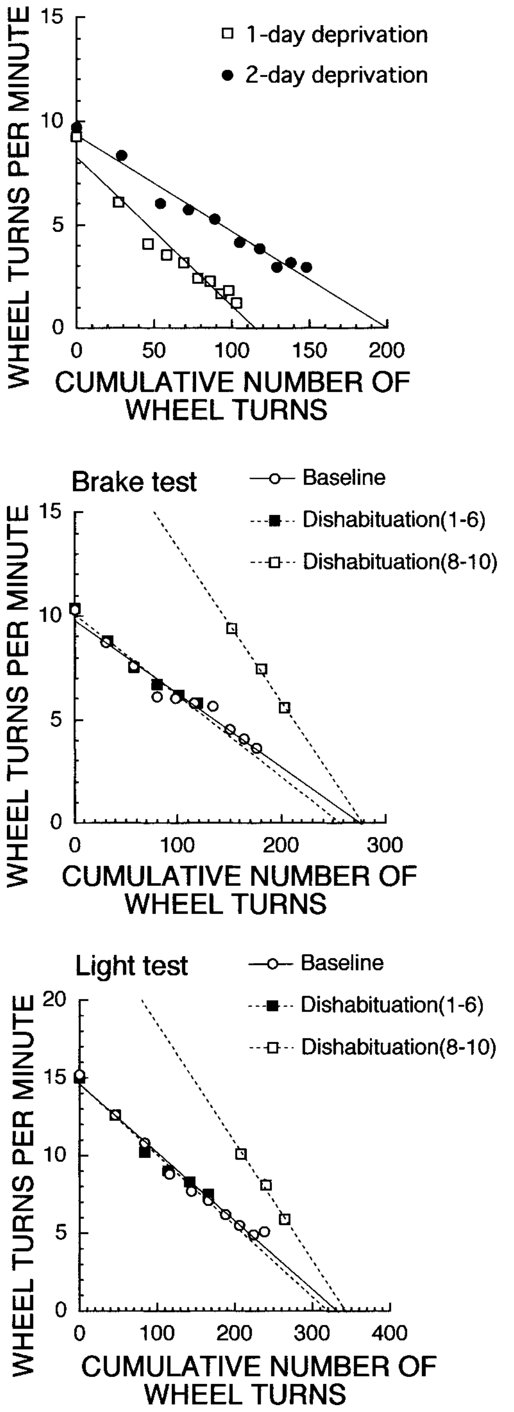

Fig. 5. Mean response rate (number of wheel turns per minute) as a function of cumulative number of wheel turns. Each point represents the cumulative number of wheel turns made just before the beginning of a 3-min block and response rate in that 3-min block. The top graph represents the application of Equation 3 to the data from Experiment 1. The middle and bottom graphs represent the application of Equation 3 to the data from Experiment 2. The regression lines for dishabituation sessions were calculated separately before (filled square) and after (open square) the dishabituating events.

portunity to run. He found a gradual within-session increase rather than a decrease, both in operant responding and in running during the reinforcement period. The sensitization-habituation hypothesis of McSweeney and Swindell (1999) can account for the discrepant outcomes in free running versus operant responding reinforced by the opportunity to run. In Belke's experiments, the reinforcement period was initiated by retraction of the lever and release of the brake. The reinforcement period was terminated by application of the brake and extension of the lever. These manipulations are reminiscent of the dishabituating events used in Experiment 2, and thus it is plausible to assume that repeated presentation of these manipulations in Belke's experiments produced dishabituation or sensitization that contributed to within-session increases in responding. Indeed, some authors attribute dishabituation to sensitization, not to the simple release from habituation that its name implies (e.g., Groves & Thompson, 1970). It is possible, therefore, that a common mechanism underlies the apparently conflicting results of Belke's experiments and those of present study.

McSweeney et al. (1996) argued that habituation also contributes to the within-session changes in responding that occur when animals respond for food on operant procedures. If this is so, and if habituation does contribute to the control of wheel running, then within-session patterns of wheel running should be similar to those of operant responding for food. A common process (i.e., habituation) should contribute to the regulation of both kinds of behavior.

Consistent with this hypothesis, the within-session patterns of wheel running shown in this study are similar to the within-session patterns shown in operant behavior under high-rate schedules of food reinforcement in other studies (e.g., Aoyama, 1998; McSweeney, Roll, & Weatherly, 1994). For example, both types of behavior are described by Equations 1 to 3. Furthermore, the effects of the present experimental manipulations are similar for the two types of responses. Similar to the results of Experiment 1 for wheel running, altering the duration of food deprivation alters initial response rate little, but does alter the late-session decreases in responding under a continuous reinforcement schedule for food (Aoyama, 2000). Similar to Experiment 2, presenting a dishabituating event alters the y-axis intercept and the slope but not the x-axis intercept of Equation 3 when rats respond on a fixed-ratio 4 schedule for food (Aoyama & McSweeney, 2001). In addition, as in Experiment 2, responding for food returns quickly to baseline levels once the dishabituating event ends (Aoyama & McSweeney, 2001; McSweeney & Roll, 1998).

Many different forms of behavior have been included under the heading of *motivation.* Traditional theories of motivation have had difficulty accounting for both ingestive motives that appear to be based on physiological deficits (e.g., feeding) and noningestive motives that do not seem to be based on these deficits (e.g., curiosity). The present study suggests that the well-known process of habituation may help to explain both types of behavior. The results show that habituation provides a better explanation for the regulation of one noningestive motivated behavior, running, than its usual explanation, fatigue. The role of habituation in the control of the ingestive motive already is well established (e.g., Swithers & Hall, 1994). Additional experiments are needed to extend this analysis to other types of motivated behavior.

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