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Timing and the Control of Variation

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Two rat experiments shed light on how variation in behavior is regulated. Experiment 1 used the peak procedure. On most trials, the 1st bar press more than 40 s after signal onset ended the signal and produced food. Other trials lasted much longer and ended without food. On those trials, the variability of bar-press duration increased greatly after the 1st response more than 40 s after signal onset. In Experiment 2, which asked whether the increase was due to the omission of expected reward or the decrease in reward expectation, reward expectation had a strong effect on response duration, whereas omission of expected reward had little effect. In both experiments, response rate and response duration changed independently, suggesting that they reflect different parts of the underlying mechanism. In Experiment 1, response durations implied that timing of the signal was more accurate than the rate-vs.-time function might suggest. Experiment 2 suggested that lowering reward expectation increases variation in response form.

Staddon and Simmelhag (1971) compared instrumental learning to evolution by natural selection. The study of evolution has emphasized both variation, which generates new genotypes, and selection, which chooses among them (Patterson, 1999), but the study of instrumental learning has been more one-sided: It has been almost entirely about selection—how reward amplifies a subset of existing behavior. Little is known about variation—what controls the variability of the behavior from which reward selects. Mackintosh (1974), for instance, devoted more than 200 pages to instrumental learning but did not mention the topic. More recent surveys (e.g., Domjan, 1996) have the same gap. With one exception (see below), empirical generalizations about instrumental learning have been rules of selection, statements about how reward increases the probability of the actions it follows. Yet the success of instrumental learning requires that variation be properly controlled. If variation is too low, an animal may never make the right (rewarded) response. If variation is too high, it may never make the right response twice. Therefore there is an optimal amount of variation, which changes as the costs and benefits of variation change. The experiments described here suggest new generalizations about how variation is controlled and provide a new way to study the subject.

The one well-established generalization about variation is that it increases during extinction (Balsam, Deich, Ohyama, & Stokes, 1998). Not all examples of this rule are interesting. Because selection reduces variation on the dimensions used to select, it is inevitable that a relaxation of selection will increase variation on those dimensions. However, many instances in which extinction increased variation, such as those involving response duration (Margulies, 1961; Millenson & Hurwitz, 1961), displacement (Herrick, 1965; Herrick & Bromberger, 1965), latency (Stebbins & Lanson, 1962), and force (Notterman, 1959), cannot be explained this way and invite further investigation. In these experiments, extinction differed from other phases in several ways: lower response rate, more omission of expected rewards, lower reward density, and lower expected reward density. Which difference caused the variation increase? The experiments reported here help choose between these possibilities.

Our original goal was different—to learn whether response rate and response duration are independent. This outcome follows from two assumptions, one about structure, the other about measurement. The structural assumption is that the underlying mechanism can be divided into two parts, each of which can be changed without changing the other: (a) a portion that decides whether to respond (press the bar) and (b) a portion that carries out decisions to respond, that is, that chooses the form of the response and makes the response. The existence of distinct "sensory" and "motor" areas in the mammalian brain (Nauta & Feirtag, 1986) supports this assumption. The measurement assumption is that response rate is sensitive to changes in the first part (decision) but not the second (execution), whereas response duration is sensitive to changes in the second part but not the first. If both assumptions are true, it should be possible to change response rate without changing response duration, and vice versa. Observation of this outcome would support both assumptions, telling us about the structure of the underlying mechanism and how its parts can be separately studied (e.g., Roberts, 1981, 1993; Sternberg, 2001).

The available evidence supports the independence of rate and duration. In a few experiments that simultaneously measured rate and form, treatments that changed rate left form unchanged (Roberts, 1987). However, the evidence need not be so limited. Because the two processes—(a) deciding whether to do something and (b) carrying out that decision—are obviously different, many treatments should change them in different ways and, thus, change rate and form (in particular, duration) differently.

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If rate and form are independent, there is room for improvement in how instrumental behavior is studied. Some popular procedures (e.g., Skinner box) measure rate but not form; others (e.g., runway) measure form but not rate. None measures both. A procedure that measures only half of the underlying processing can easily miss something important.

The experiments reported here measured both. The rate measure was how often the bar was pressed (response rate, abbreviated *rate*); the measure of form was how long the bar was held down (response duration, abbreviated *duration*). Because the time between responses was usually 5–20 s and durations were usually 0.1–0.5 s, large changes in duration had no detectable effect on rate.

Experiment 1

The goal of this experiment, which used the peak procedure, was to test the prediction that rate and duration are independent. On most trials, food was given for the first bar press after a fixed time (40 s) from the start of the signal (light or sound). When food was given, the signal ended. On other trials, the signal lasted much longer and ended without food. This produced a wide range of rates, making a correlation between rate and duration easy to see.

Method

The experiment was done in two replications. The replications were the same in all respects under our control except that they used different subjects, occurred at different times of day, and lasted different numbers of days. The second replication was done to confirm the results of the first replication. It lasted many more days to give more precision, in case some analyses required it.

Subjects. In each replication, the subjects were 18 male rats (Rattus norvegicus; Charles River laboratories, CD strain) with several months experience with the peak procedure. In the first replication, the rats were about 19 months old at the start of testing; in the second, about 6 months. All subjects were housed separately and given free access to water. Each rat was given about 12 g of food each day shortly after the experimental session.

Apparatus. The rats worked in 18 similar lever boxes. Four were 23 cm × 20 cm × 28 cm; six were 23 cm × 20 cm × 21 cm; and eight were 28 cm × 26 cm × 28 cm (Gerbrands Series 7400 operant test chambers, Arlington, MA). The roof and side walls of the box were transparent acrylic; the front and back walls were aluminum. A pellet dispenser delivered 45-mg pellets (BioServ mix T101, Frenchtown, NJ) to a food cup that the rat accessed through a hole in the center of the front wall. Each box contained a lever that was available to the rat throughout the session and required a force of about 15 g to operate. Each box was enclosed in an insulated wooden chamber designed to attenuate outside light and sound; eight of the chambers were Gerbrands G7211 (Arlington, MA) enclosure, side opening. There was a fan for ventilation. A small lamp (General Electric 1155X, Cleveland, OH) was mounted on the side of each box; it provided the light stimulus. The sound stimulus was white noise from 5-cm speakers, which raised the sound level from about 65 to 69 Db (A scale) in the 10 smaller boxes and from 54 to 67 Db in the 8 larger boxes. A PDP 11/23 computer (Digital Equipment Corporation, Maynard, MA) controlled the experimental events and collected the data. It checked the position of the lever 10 times per second. A response was recorded when the lever switch was closed (lever down) and then opened (lever up).

Procedure. Intertrial intervals (ITIs) were dark and silent. Trials began with either light onset or sound onset; for each rat, light and sound trials were equally likely. Except for the stimulus difference, they were the same. A random 80% of trials were food trials, which ended (signal offset) with a food pellet when the rat made its first response more than 40 s after signal onset. The remaining 20% were empty trials, which lasted 195 s plus a geometrically distributed addition that averaged 50 s in length (it ended with 0.1 probability each 5 s) and ended without food. (We used both light and sound as signals for diagnostic reasons, partly because light bulb failure would produce different results than other failures and partly because the two signals might produce interesting differences in behavior.) ITIs lasted 20 s plus a geometrically distributed addition that averaged 20 s in length (it ended with 0.1 probability each 2 s). The experiment was run 7 days per week. The daily session lasted 6 hr. In the first replication, the session started between 7 AM and noon; in the second replication the session started between 1 PM and 7 PM. The first replication lasted 48 days; the second replication lasted 124 days.

Data taken. To be counted as a response, a bar press had to close the lever switch and reopen it in 2.9 seconds or less; durations of 3 s or more were excluded (in retrospect, a mistake) because of the worry that they might be generated by a different mechanism. Responses were recorded during the last 20 s of the ITI and the first 195 s of each trial. Both the time (in seconds, measured from the start of the trial) and the duration (in tenths of a second) of each response was recorded. Trials with no responses during the recording interval (e.g., because of equipment failure) are not included in the analyses. Such trials were 1.2% of all trials in Replication 1 and 0.6% of all trials in Replication 2.

Data analysis. Average durations were computed in three steps. First, response data for each rat was cumulated across all days in the experiment. Second, the harmonic mean was computed over the durations for each rat. We used the harmonic mean because the distribution of response durations resembled an exponential distribution (see Figure 1). Third, an average was

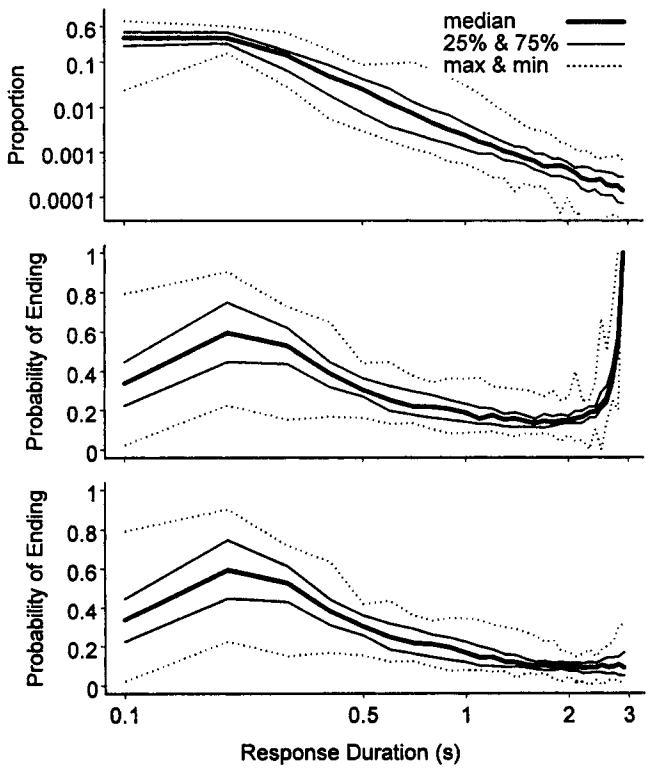

Figure 1. Experiment 1: Distribution of response durations. Sample sizes per rat ranged from about 15,000 to 98,000 for Replication 1 and from 57,000 to 462,000 for Replication 2. max = maximum; min = minimum.

computed across rats. Trimmed means were used to average across rats when some of the numbers being averaged were based on relatively little data, raising the chances of outliers; otherwise, arithmetic means were used. In Figures 1 and 5, medians were used because of some infinities.

Rate calculations excluded responses on food trials made after the 40th s. Inclusion of these responses would have made it impossible to calculate exact rates.

Statistical tests used a significance level of .05.

Results

The first replication recorded 0.7 million bar presses; the second replication recorded 2.8 million. We found no important differences between the two replications, so the following results usually combine them.

The top panel of Figure 1 shows the distribution of bar-press durations on a log–log scale. Apart from the shortest duration (0.1 s), the distribution was close to linear. The middle panel has the corresponding hazard function (e.g., Luce, 1986), which gives the probability that a bar press will end during a time interval (100 ms wide) if it has lasted until then. For example, if a hazard function has a value of 0.1 at a duration of 500 ms, it means that 10% of the responses with durations of at least 500 ms had durations less than 600 ms. The rise at longer times is no doubt due to the artificial cutoff; responses longer than 2.9 s were not recorded. Assuming that the hazard function is actually flat at long durations, the proportion of bar presses not recorded can be estimated by determining what value of that proportion produces this outcome. The bottom panel of Figure 1 shows that it is about 0.14%, about 1 in 1,000.

Independence of rate and duration. Figure 2 shows how rate (upper panel) and duration (lower panel) changed during a trial. The most interesting result was the increase in duration that began at about the time of food; it is studied in detail below. Although individual durations were measured to a precision of 100 ms—possible durations were 100 ms, 200 ms, and so forth—Figure 2 shows much smaller differences because of the large amount of data.

Figure 3 shows duration versus rate. Each point is from a different time during the trial. Before averaging over rats, we normalized the rate and duration functions. We divided the y values of the rate functions by the function's maximum y value (the maximum rate) and multiplied by 100. We normalized duration functions by subtracting from each duration the minimum duration, dividing the result by the range of the durations (maximum − minimum), and multiplying by 100. Figure 3 shows that rate and duration were not tightly coupled, that is, a big change in one could be accompanied by little or no change in the other. For instance, Seconds 16–17 and 94–103 (Replication 1) produced very different durations but similar rates. Seconds 1–7 and 61–62 (Replication 2) produced very different rates but similar durations.

Nature of the duration increase. Figure 4 shows percentiles (10th, 50th, and 90th) of the duration distribution as a function of time since omission (short for reward omission), that is, time since the first response after Second 40, which is what triggered the increase. The percentiles were computed separately for each rat, then averaged over rats. The 90th percentile increased far more than the 10th percentile, even when the comparison was made in percentages. From Second 0 to Second 50, the 90th percentile increased 175 ± 22 percent, whereas the 10th percentile increased 32 ± 5 percent, reliably less, $t(35) = 7.66$.

Figure 5 shows whole distributions. The upper panel shows the effects of omission. After omission, the distribution became much wider. The change was very large (the probability of the longest durations increased by a factor of more than 150) and would be reliable whatever statistical test was used. In later analyses, we wanted to test for a similar difference between distributions with as much sensitivity as possible, so we used the difference shown in the upper panel of Figure 5 to learn

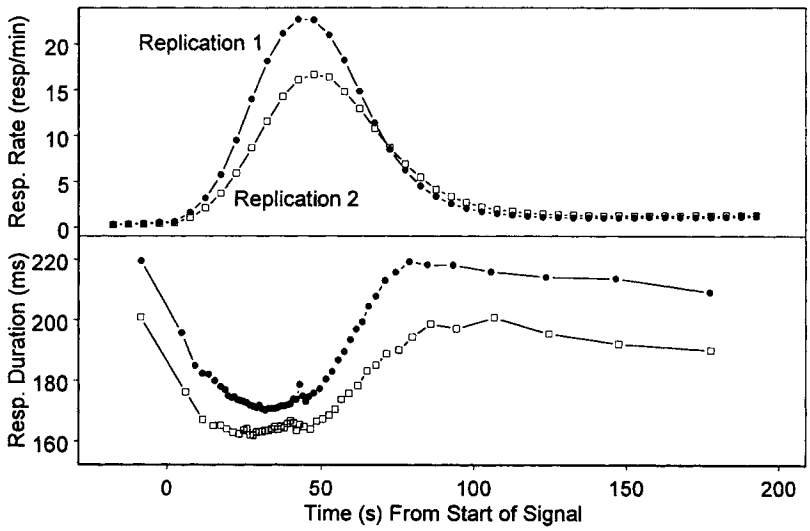

Figure 2. Experiment 1: Response rate (upper panel) and response duration (lower panel) as a function of time since the start of the signal. Points in the duration function are unequally spaced along the time axis so that each point will represent roughly the same number of responses. Each point in the lower panel is based on about 4,000 (Replication 1) or 8,000 (Replication 2) responses per rat. Resp. = response.

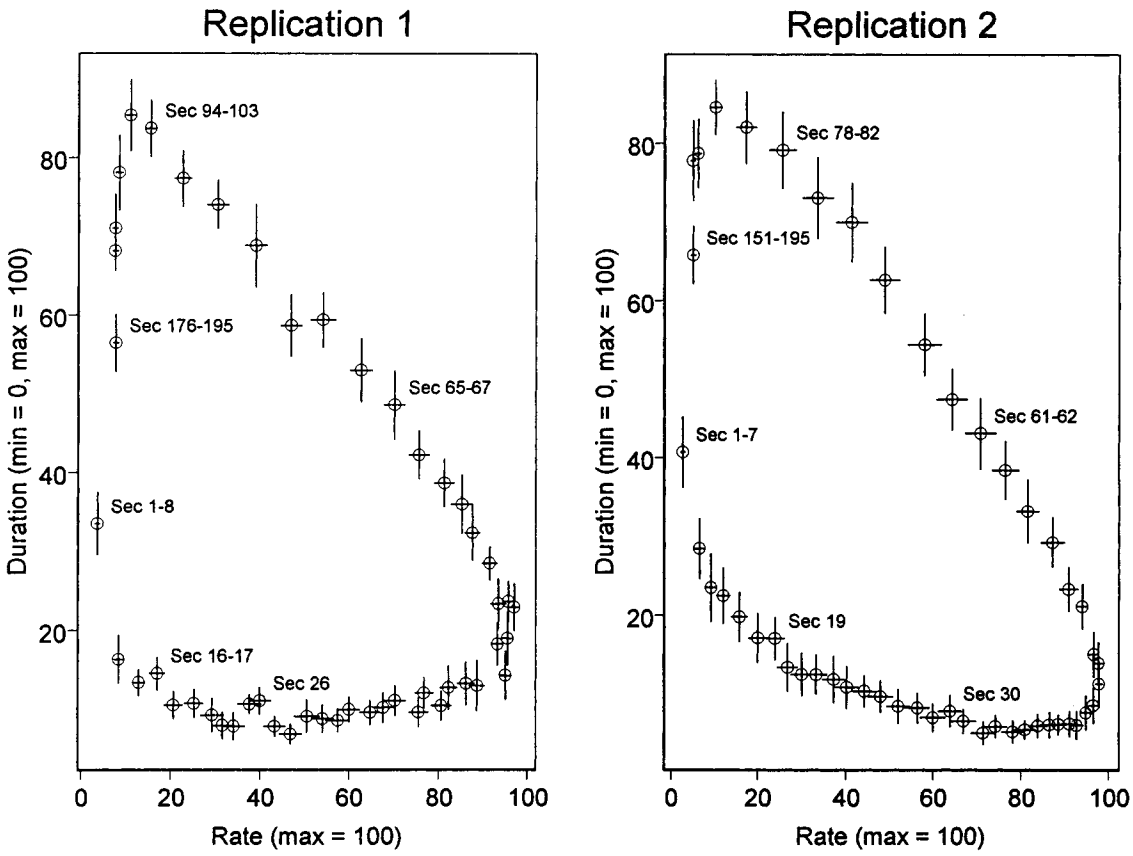

Figure 3. Experiment 1: Response duration versus response rate. The function has 50 points; each is from a different time period since the start of the signal. Each value is a 10% trimmed mean over 18 rats; error bars show standard errors. To reduce the effect of individual differences, both measures were standardized before averaging over rats. The rates of each rat were standardized by (a) dividing each rate by the maximum rate for that rat, then (b) multiplying by 100. The durations of each rat were standardized by (a) subtracting from each duration the minimum duration for that rat, (b) dividing the result by the difference between the maximum and minimum for that rat, and (c) multiplying by 100. The time periods were adjusted so that for each replication there were roughly the same number of responses for each point; this is why some time periods cover only one second, whereas others cover several seconds. min = minimum; max = maximum.

which statistic reveals it most clearly. We considered 10 ways to summarize the distributions, two measures (mean and standard deviation) each applied to five transformations of the data: no change, square root, logarithm, reciprocal square root, and reciprocal (Tukey, 1977). The summary that revealed the difference most clearly was the mean of the logarithms, $t(35) = 18.29$. All later analyses used this combination of mean and logarithm to detect differences between distributions.

The widening diminished with time (lower panel of Figure 5). During Seconds 100–150 after omission, the distribution was narrower than during Seconds 45–75, $t(35) = 11.00$.

Cause of the duration increase. The duration functions in Figure 2 confound two factors. Responses after Second 40, when the increase began, were both (a) often after food omission (i.e., after the first response after Second 40) and (b) later in the trial. To separate these two factors, Figure 6 shows duration as a function of time for (a) responses before omission (i.e., all responses up to and including the first response after Second 40) and (b) responses after omission (i.e., all responses after the first response after Second 40, which occurred only on empty trials). Figure 6 suggests that preomission durations did not increase after the time of food but that postomission durations did.

To judge the reliability of this observation, we fit a straight line separately to the results from each rat. Using responses before omission, we computed average response durations for Seconds 41–45, 46–50, 51–55, and 56–60 (four averages per rat). Then we fit a line to the function giving duration as a function of time into the signal. This produced one slope per rat; the average slope over rats was -0.7 ± 0.2 ms/s, reliably negative, $t(35) = 2.91$. The same calculations using responses after omission gave an average slope of 0.9 ± 0.1 ms/s, reliably positive, $t(35) = 6.19$. This shows that omission, not the passage of time, caused the rise in response duration seen in Figure 2. The preomission function in Figure 6 also shows that a low response rate is not always associated with a high response duration. If a rat made its first response after Second 40 at Second 60, the interresponse interval was at least 20 s, equal to a response rate of three responses per minute or less.

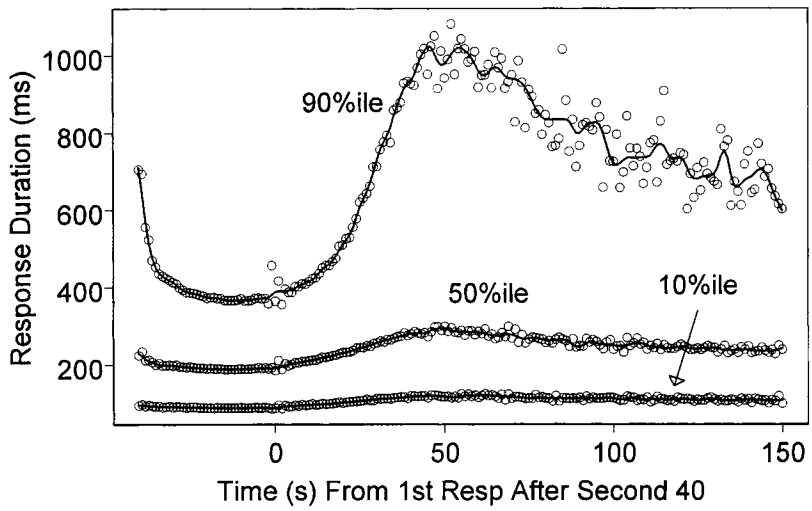

Figure 4. Experiment 1: How food omission changed the spread of the distribution of response durations. Each point is a 10% trimmed mean over 36 rats. Resp = response.

Yet the duration of preomission responses after Second 40 was less than the duration of earlier preomission responses.

To display more clearly the effects of omission, Figure 7 shows rate (upper panel) and duration (lower panel) as a function of time before and after omission. Only data from empty trials were used, so that all data points are based on exactly the same trials. We normalized rate and duration before averaging over rats. We normalized rate by dividing all rates for each rat by that rat's average rate 2–5 s after reward omission and multiplying by 100. We normalized duration by dividing each duration by the duration of the first response after Second 40 and multiplying by 100. The obvious effect of omission on duration was the increase that starts close to Second 0 and lasts at least 40 s. But two other effects are worth noting. First, duration at Second 1 was higher than at Second 0, $t(35) = 2.84$. Second, durations at Seconds 3–5 were longer than extrapolation from later times would predict. To show this, the lower panel of Figure 7 includes a straight line fit to the results from Seconds 10–30. After about Second 10, the results are close to the line; before Second 10, they are above the line. To judge the reliability of this change, we fit straight lines to the data from Seconds 3–9 (one line) and Seconds 10–30 (another line) and compared the two slopes, doing this for each rat. The later (Seconds 10–30) lines were steeper than the earlier (Seconds 3–9) lines, $t(35) = 2.69$.

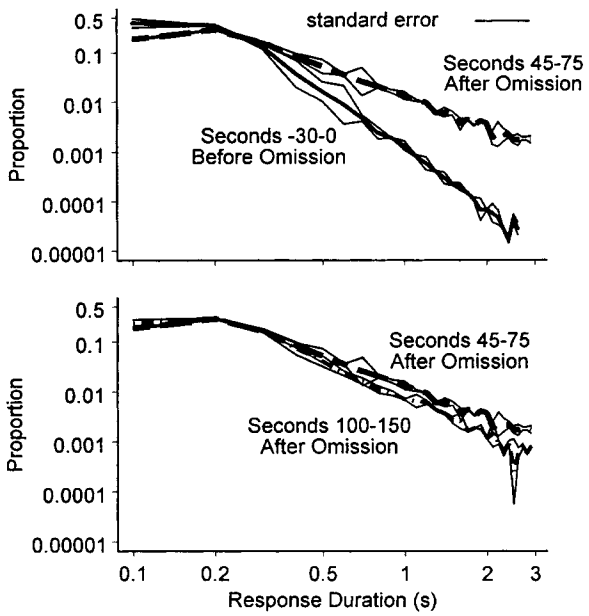

Figure 5. Experiment 1: How food omission changed the distribution of response durations. The upper panel shows the initial effect; the lower panel shows the flattening produced by food omission diminished with time. (Each point is a median over 36 rats. Standard errors were computed using the jackknife.)

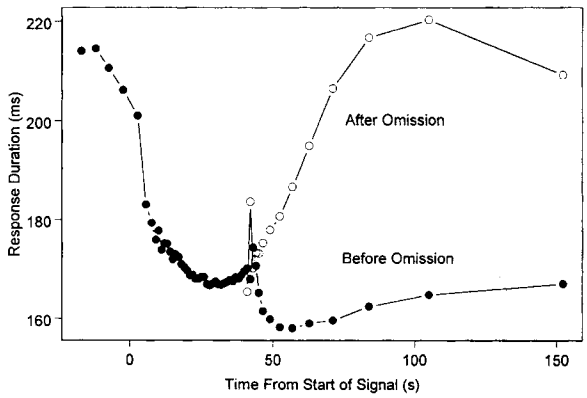

Figure 6. Experiment 1: Response durations before and after omission as a function of time from the start of the signal. First response after omission equals second response after 40 s on empty trials. Responses before omission equals all earlier responses on empty trials and all responses on food trials. The points are spaced so that each preomission point is based on about 12,000 responses.

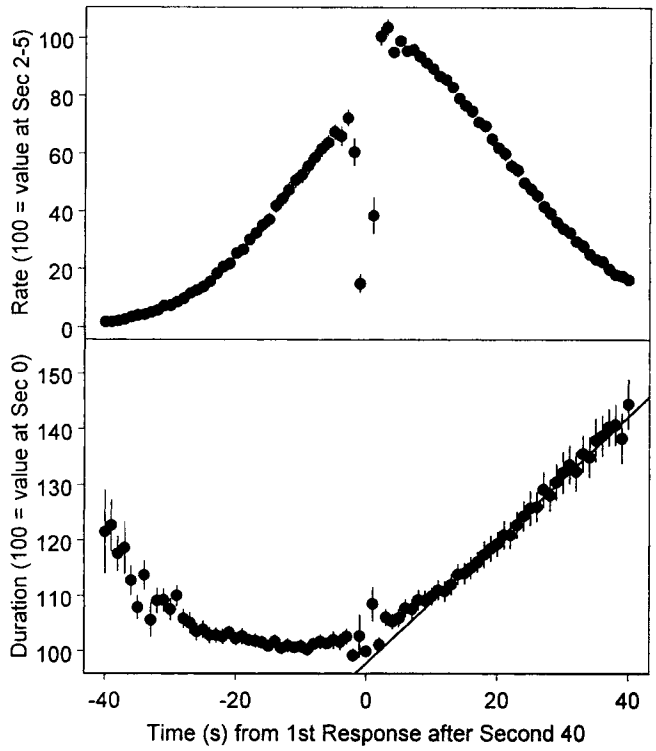

Figure 7. Experiment 1: Response rate (upper panel) and response duration (lower panel) as a function of time before and after the response that revealed the absence of food. The response at Time 0 is the first response after Second 40 on empty trials. All of the data came from empty trials—about 900 trials per rat in Replication 1, about 2,900 trials per rat in Replication 2. Each average is a 10% trimmed mean over 36 rats; error bars show standard errors. Sec = second.

The effects of omission on duration shown in the lower panel of Figure 7—the differences between before and after Second 0—might be due to (a) making a response, (b) making a response not followed by food, or (c) making a response not followed by expected food. To allow us to choose between these possibilities, Figure 8 shows the same analysis done with earlier responses. The upper panel shows response duration before and after Second 25 on those trials when there was a response at Second 25; the lower panel shows the same thing for responses at Second 30. Because expectation of food was greater after Second 40 than before Second 40, effects of unmet expectations should be larger after the first response after Second 40 (lower panel of Figure 7) than after earlier responses (Figure 8). In contrast, effects due to making a response or making a response not followed by food should be the same size. Comparison of the lower panel of Figure 7 and Figure 8 suggests several conclusions:

1. The long-lasting increase depends on expectations. Fitting a straight line to the scaled durations for each rat from Times 6–10 s after the target response (8 durations) gives an average slope of 0.7 ± 0.1 %/s when the target response was the first response after Second 40 (lower panel of Figure 7), $t(35) = 4.68$. In contrast, there was no detectable positive slope when the target response was at Second 25 (upper panel of Figure 8), 0.0 ± 0.2 %/s, $t(35) = 0.25$, or at Second 30 (lower panel of Figure 8), 0.2 ± 0.1 %/s, $t(35) = 1.60$. Slopes after the first response after Second 40 were larger than slopes after Second 25, $t(35) = 3.32$, and slopes after Second 30, $t(35) = 3.28$.

2. The very brief increase (1 s after the response) does not depend on expectations, because the size of the increase was roughly the same at all three times (Second 25, Second 30, and the first response after Second 40), $F(2, 70) = 0.71$.

3. The brief increase (about 3–10 s after the response) depends on expectations. In the lower panel of Figure 7, responses 3–5 s after the target response lasted 6.0% ± 1.3% longer than the target response, $t(35) = 4.74$. This effect was not present after Second 25 (upper panel of Figure 8); the increase was 0.9% ± 1.0%, $t(35) = 0.99$. It was barely present after Second 30 (lower panel of Figure 8); the corresponding increase was 1.9% ± 0.8%, $t(35) = 2.30$. The small effect at Second 30 was not due to an increase in the likelihood that later responses were 1 s after another response, because it persisted when all such responses were removed, $t(35) = 2.96$. The increase after the first response after Second 40 was larger than the increase after responses at Second 25, $t(35) = 4.60$, and Second 30, $t(35) = 3.75$.

Did the internal effect of reward omission (whatever triggered the long-lasting duration increase) continue to build with each successive unrewarded response, as the rat became more and more confident that food would not be available, or was a single unrewarded response (at the appropriate time) enough to trigger the full reaction? Figure 9 helps choose between these two possibilities. It shows the same data plotted two ways. The data has the structure of a two-way table, with response number (eight levels) and time from omission (two levels) as factors. Durations were computed separately for the first, second, third, and following responses after food omission (i.e., the second, third, etc., responses after Second 40). For each response number, two durations were calculated: early half and late half. For each response number (first, second, third, etc.), the median time from omission was calculated. Responses before the median time were early half; responses after the median time were late half. This division was done separately for

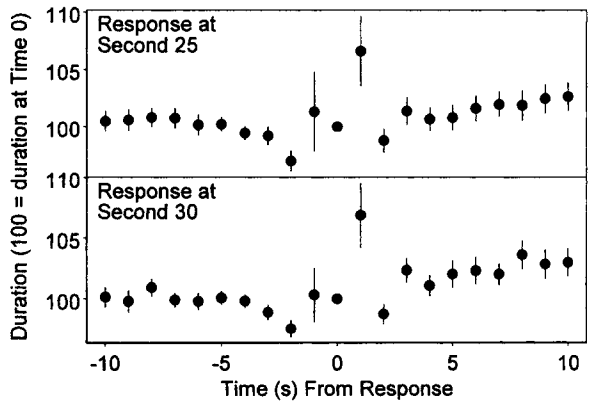

Figure 8. Experiment 1: The effects of reward omission before Second 40 on response duration. The upper panel shows behavior before and after a response at Second 25; the lower panel, after a response at Second 30. In the upper panel, the results are based on about 400 trials per rat in Replication 1 and about 1,900 trials per rat in Replication 2. The corresponding values for the lower panel are 600 and 3,100. Each average is a 10% trimmed mean over 36 rats; error bars show standard errors.

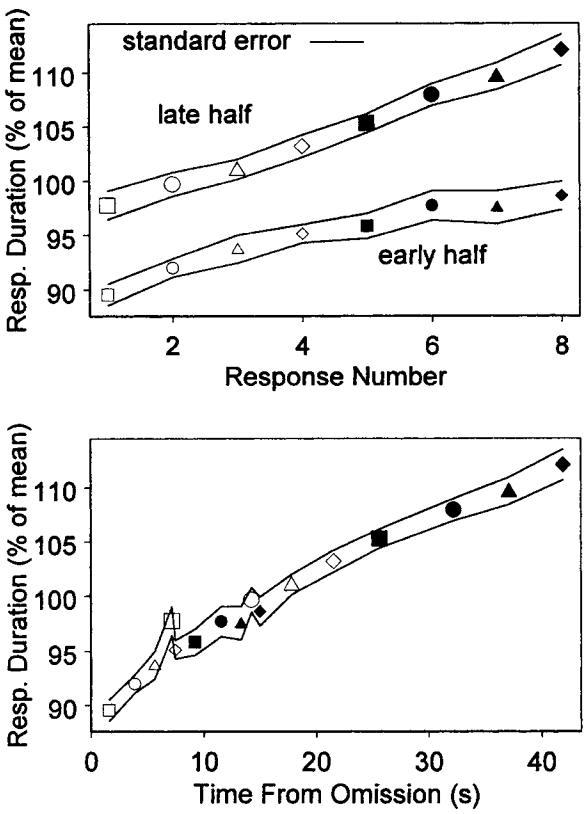

Figure 9. Experiment 1: Postomission response durations as a function of response number and time from omission. The upper and lower panels show the same data. The plotting symbol indicates the response number; the size of the symbol, the time. The first response after omission—which is the second response after Second 40 on empty trials—has response number = 1, the second response has response number = 2, and so forth. The two points for each response number were determined as follows: Responses were pooled over all rats and divided into halves on the basis of time of occurrence, early half and late half. The median times calculated from all rats was used to divide the responses for each rat. For each rat, the responses in each half were used to compute an arithmetic-mean time since omission and a harmonic-mean response duration. Then the response durations for each rat were normalized by dividing by the mean of the 16 durations for that rat—2 halves by 8 response numbers. The plotted times and durations are 10% trimmed means over 36 rats. Resp. = response.

each rat. The two possibilities described above make different predictions about the importance of the two factors (response number and time since omission). According to the first hypothesis, the internal effect of omission increased with time from omission because more and more responses were made, further confirming the absence of food. If so, duration should vary with response number; with response number held constant, duration should be unaffected by time from omission. According to the second hypothesis, the internal effect of omission increased with time from omission because of a process that was fully engaged by the first unrewarded response after Second 40. If so, duration should vary with time from omission; with time from omission held constant, duration should be unaffected by response number.

These predictions can be tested by plotting the data two different ways (Figure 9)—with response number (upper panel) or time from omission (lower panel) as the abscissa. The first idea predicts that results will lie along a single line in the upper panel but not the lower panel. The second predicts the reverse: a single line in the lower panel but not the upper panel. The actual results are very close to the predictions of the second idea. The variation in these 16 (average) response durations is almost entirely explained by when the responses were made; response number explains less of the variation. Examination of results for individual rats confirms the impression given by Figure 9. To choose between the two predictions for each rat, we fit a quadratic function to the 16 durations using either response number or time from omission as the independent variable. For 29 of the 36 rats, the fit, judged by the sum of the squared residuals, was better with time from omission than with response number (sign test, $p = .0003$). Fitting linear functions rather than quadratic functions produced the same result. This suggests that the first unrewarded response after Second 40 was sufficient to produce the maximum effect of omission.

Discussion

Independence of rate and duration. Figure 3 shows that rate and duration were independent over a wide range. This supports the two assumptions that predicted this result: (a) the underlying mechanism has two separate parts, and (b) rate selectively measures one part, and duration selectively measures the other. If rate and duration measure different processes, then duration provides information about the underlying mechanism that rate cannot.

Long-lasting duration increase. The long-lasting increase in duration after Second 40 (lower panel of Figure 2) was not predictable from any previous effect. It had three unusual features. First, it was very clear, $t(35) = 18$ (upper panel of Figure 5). New effects this strong are rare. Second, it had no obvious benefit, unlike effects of similar strength. It is beneficial for an animal to adjust its response rate when the probability of reward changes, to avoid tastes followed by illness, and so on. The benefit of the duration increase is less clear. Third, it involved a large, more-than-proportional increase in variability. The whole effect could be described as an increase in variability, because the 10th percentile of the duration distribution barely changed, whereas the 90th percentile of the distribution more than doubled (Figure 4).

Lightning does not strike three times in one place for different reasons, so these three features should have one explanation. All three are understandable if the increase in duration reflects regulation of variability—a mechanism that adjusts variability according to recent events. A new effect can be very strong because the topic (control of variability) has barely been studied; there are strong effects left to find. The effect has no obvious benefit, because the benefit conveyed by variability is not obvious—theories of optimal behavior, for instance, routinely ignore it (see Charnov, 1976, for many examples). The effect involved a large increase in variability (larger than usual, given the change in mean) because the function of the effect is to increase variability, to spread a wider net from which reward selects.

That the duration increase diminished later in the trial, 100–150 s after omission (lower panel of Figure 5), is more evidence that the duration increase was not caused by a rate change. The large increase in duration (from time of omission to 45–75 s after omission) was accompanied by a decrease in rate. If the rate change caused the duration change, then a decrease in duration

should be accompanied by an increase in rate, but no such increase occurred (Figure 2). Regulatory mechanisms designed to make fast corrections often overshoot the mark when changing from one level to another.

Precision of timing. The rats apparently timed the interval more precisely than the width of the response-rate functions (upper panel of Figure 2) would suggest. To believe that the width of the response-rate function indicates the precision of timing is to assume that each bar press is a guess that reward is available. Only on a small fraction of trials does the rat believe that reward is available for a response at, for instance, Second 10, but when it responds at that time, its expectation of food is the same as when it responds at Second 30. In other words, the rat's expectation of reward should be the same after every response, and the reaction to the disappointment of that expectation should be the same. This was not true. The long-lasting rise in response duration after food omission (Figure 7) was triggered much more by responses after Second 40 than by earlier responses (Figure 8).

Not only did food omission before Second 40 have little effect, food omission after the first response after Second 40 had little effect (Figure 9). The second, third, fourth, and following responses after Second 40 apparently added nothing to the rats' belief that no food would be given on that trial. Yet many responses were made after the first response after Second 40 (upper panel of Figure 7). Therefore, the conclusion that the rats timed the signal more precisely than the rate functions indicate is supported by behavior at two different times (before and after the peak in the rate function) and two types of evidence (Figures 8 and 9).

Short-lasting duration increase. Omission effects have been familiar, of course, since Amsel and Roussel (1952) reported that rats ran faster in the second alley of a double runway when expected food was missing from the first goalbox, which they called a *frustration effect.* The long-lasting duration increase, although triggered by the omission of expected reward, lasted longer (at least 120 s) than the runway effect, which disappeared when rats were confined to the first goalbox for 90 s (MacKinnon & Amsel, 1964). If the two effects involved the same mechanism, the runway effect should, if anything, have lasted longer, because the omitted reward was larger. Such a sizeable difference suggests a different mechanism. However, the short-lasting duration increase, which Figure 7 suggests lasted less than 10 s (see Experiment 2 for a much clearer view), can be plausibly attributed to the same mechanism as the runway effect.

Experiment 2

The increase in duration variability (Figure 4) began when the usually rewarded response (the first response after Second 40) was not rewarded. Not only was this "frustrating" (in the sense of Amsel & Roussel, 1952), it implied no reward for several minutes (the rest of the signal and the ITI). The decline in rate after omission (upper panel of Figure 7) showed that the rats learned this absence. Therefore, the increase started when (a) an expected reward failed to occur and (b) expectation of reward on the current trial decreased. Which caused the increase in duration variability?

Both possibilities are plausible. (a) *Omission of expected reward.* According to Balsam et al. (1998), "disappointment increases variability" (p. 407). Reward omission has many effects (Papini & Dudley, 1997); an increase in variability might be one of them. (b) *Lower expectation of reward.* Cost of variation usually depends on the likelihood of reward. An increase in variation reduces the rate of the most frequent responses and increases the rate of less frequent responses. Usually, the more frequent responses are the more productive ones, so an increase in variation reduces short-term payoff. If expected short-term payoff goes down, the expected cost of variation goes down—there is less to lose. When the cost of variation goes down, the optimum amount of variation should increase.

This experiment helped us to choose between these two possible causes by measuring their effects separately. Like Experiment 1, there were trials defined by light or sound and separated by long ITIs. The first response during a signal turned off the signal and usually but not always produced food. Between trials, there was a lean schedule of reward (variable interval 100 s).

The first response during the signal produced reward so that the density of reward, and therefore expectation of reward, during the signal would be as high as possible. The greater the expectation of reward, we assumed, the larger the effect of its omission. We measured the effect of omission by comparing behavior after trials that ended with food with behavior after trials that ended without food. Expectation of reward was presumably the same in both cases, because both were measured during the ITI.

We measured the effect of reward expectation by comparing responses during the trial (80% rewarded) and ITI responses (few rewarded). Because reward omission turned out to have no detectable effect, it was also interesting to compare behavior during the ITI after an ITI response had been (a) rewarded and (b) unrewarded. The change in expectation produced by one event (reward/nonreward) might have a detectable effect.

Method

Subjects. The subjects were 18 naive male rats (Charles River Laboratories, CD strain). At the start of the experiment, they were about 3.5 months old. They were housed and fed as described in Experiment 1.

Apparatus. The apparatus was the same as in Experiment 1.

Procedure. Before beginning the experiment, all rats were given 3 days (4 hr/day) of bar-press training in the operant boxes. After training, one signal (light for half the rats, sound for the rest) was on continuously throughout the session. Between trials, rats were on a variable interval (VI) 100 s schedule. Food was primed (given for the next response) with a 1/100 probability each second. A pretrial period began with 1/30 probability each 6 s during intertrial intervals. It lasted 30 s and involved no change in the likelihood of reward; the VI 100 s schedule was maintained. After this period, a signal (light or sound, whichever was not the session-defining signal) came on. The first response during this signal turned it off and, on 80% of the trials, caused the delivery of one 45-mg food pellet. This was followed by an additional 120 s of VI 100 s (the posttrial period), after which the ITI began. Each session lasted 3 hr; there was one session per day, 7 days a week. The experiment lasted 51 days. Because of error, data from 3 days were not available.

Data taken. For each response, its time of occurrence (in seconds) and duration (to the nearest 0.1 s) were recorded. Responses with durations of 3 s or more were not recorded. During the first 32 daily sessions, only responses during a trial were recorded; during the last 16 sessions, responses during ITIs were also recorded. Responses during the first second of the presignal period were incorrectly recorded, leaving 29 seconds of presignal data to analyze.

Data analysis. As in Experiment 1, average durations were computed in three steps. First, data for each rat was summed over days; second, the harmonic mean was computed for each rat; finally, an average (10%

trimmed means, to ensure that changes from one average to another are not due to 1 or 2 rats) was computed across rats. As in Experiment 1, statistical tests used a significance level of .05. Analyses of variance (ANOVAs) treated rat as a random factor.

Results

About 28,000 trials and 1.3 million bar presses were recorded.

Reward omission. Figure 10 shows rate (upper panel) and duration (lower panel) before, during, and after the signal. There was no sign of the large, long-lasting increase in duration after omission seen in Experiment 1. When we used the posttrial period (45–75 s after omission) that Experiment 1 (Figure 4) suggested would show the biggest effect, there was no detectable difference between durations after reward and durations after nonreward, $t(17) = 1.64$. In percentages, the difference was 1.1% ± 0.7% (mean ± standard error). Another reasonable comparison—posttrial versus pretrial, similar to the before and after comparison of the upper panel of Figure 5—gives the same result, no difference, $t(17) = 0.12$.

Reward expectation. Reward was more expected during the signal than during the ITI. During the signal, 80% of responses were rewarded; during the last 16 days, when all responses were recorded, the median (over rats) probability of reward for ITI responses was 7% (range 3–21%). As Figure 10 suggests, durations were less during the signal than during the interval before the signal, $t(17) = 4.72$. Figure 11 (upper panel) shows the two distributions. Although the difference is smaller than the difference seen in Experiment 1 (upper panel of Figure 5), it is very clear and similar in shape to the difference in Experiment 1.

During the ITI, it is reasonable to assume that expectation of reward was more after a rewarded response than after an unrewarded response. Figure 12 shows rates (upper panel) and durations (lower panel) before and after those two events. The target responses used to compute Figure 12 were all responses (a) made more than 30 s after the end of a signal and (b) for which responses were recorded for at least 40 s after the response. About 600,000 responses (5% of which were rewarded) met these requirements.

As Figure 12 suggests, just one reward produced a small but clear long-lasting decrease in duration. Measured with responses 30–40 s after the target response, the decrease is 3.4% ± 1.1%, $t(17) = 3.16$. Figure 11 shows the two distributions. This difference did not appear during the same time period after a trial (Figure 10). When we compare responses 30–40 s after trials that did and did not end with food, we find that the decrease was 1.2% ± 0.8%, not reliable, $t(17) = 1.54$. The interaction was reliable: The ITI decrease after reward during the ITI was more than the decrease after reward at the end of a trial, $t(17) = 1.79$.

Independence of rate and duration. Rate and duration were independent three ways. (a) They were independent over the course of the experiment (Figure 13): Rate during the signal was roughly constant after a few days, but duration during the signal declined for at least 30 days. When we compare Days 2–3 with the last two days (Days 47–48), we find that rate decreased 0% ± 6%, whereas duration decreased 37% ± 4%. (b) They were independent during the signal (Figure 14): Rates were computed by determining the probability of a response each second given that the rat had not yet responded (i.e., a hazard function) and multiplying by 60 to get responses per minute. Again, rate (upper panel) and duration (lower panel) behaved differently. The maximum of the rate function was later than the minimum of the duration function, $t(17) = 4.61$. (c) Finally, they were independent before rewarded and unrewarded ITI responses (Figure 12): Rates (upper panel) differed because, of course, the probability of reward increased as response rate declined. In spite of the two-fold rate difference, the corresponding durations (lower panel) were very similar. During the 15 s before the target response, the "rewarded" rates were 54% ± 2% less than the "unrewarded" rates, whereas the "rewarded" durations were −0.1% ± 0.7% less than the "unrewarded" durations.

Short-lasting effect of reward omission. Although reward omission did not cause a large, long-lasting increase in duration, it

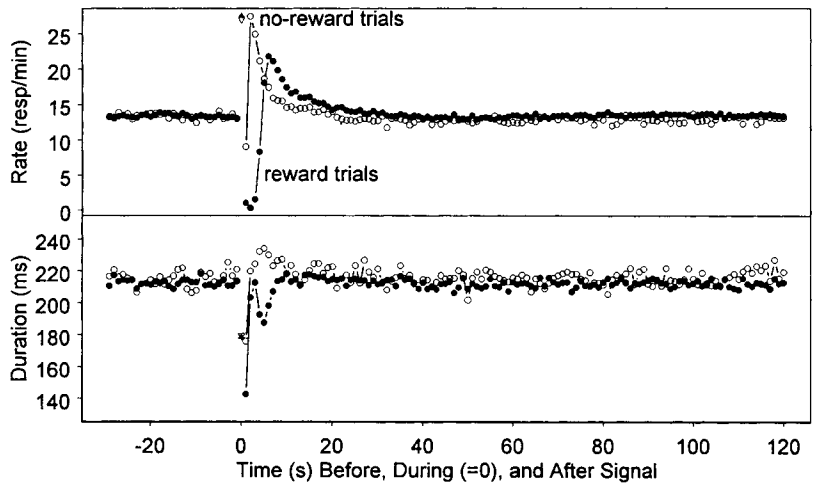

Figure 10. Experiment 2: Response rate (upper panel) and response duration (lower panel) as a function of time before, during, and after the signal. Each point is a 10% trimmed mean over 18 rats. Data during the signal are represented by triangles. Resp. = response.

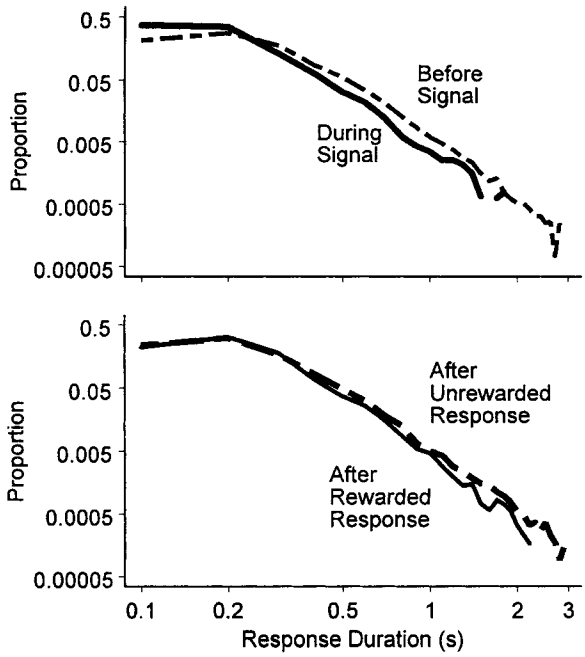

Figure 11. Experiment 2: Distribution of response durations before and during the signal (upper panel) and 30–40 s after rewarded and unrewarded responses during the intertrial interval (lower panel). Each point is a median over 18 rats.

did produce a small, short-lasting increase (lower panel of Figure 10). After a signal that ended with no reward, duration was less than usual for 1 s, then more than usual for about 8 s. To judge the reliability of these changes, we computed a baseline duration for each rat based on all responses during the presignal period and all responses during the postsignal period more than 30 s after the end of the signal. After nonreward, duration was less than baseline during Second 1, $t(17) = 2.86$, but more than baseline during Seconds 2–9, $t(17) = 4.58$.

Reward omission had the same effect during the ITI (lower panel of Figure 12). After nonreward, duration was more than usual for about 8 s, starting at Second 2. To judge the reliability of these changes, we computed a baseline duration for each rat based on all responses 5–15 s before the target response and all responses 15–30 s after the target response. An ANOVA with factors (a) before versus after the target response (2 levels), (b) target response rewarded versus not rewarded (2 levels), and (c) rat (18 levels), showed no reliable effect of before versus after, $F(1, 17) = 2.14$; no effect of rewarded versus not rewarded, $F(1, 17) = 2.73$; and no reliable interaction of these two factors, $F(1, 17) = 3.70$, so it was reasonable to combine results from these conditions into a single baseline value. After unrewarded target responses, duration was more than baseline during Seconds 2–9, $t(17) = 4.56$.

Figure 15 shows how the short-lasting effect changed with training. Neither the ITI effect nor the postsignal effect were reliable on Days 1–2, $t(17) = 1.16$ (ITI) and 0.74 (postsignal). Both were reliable for most of the later blocks of days shown in Figure 15. The critical one-tailed value of $t(17)$, 1.74, was exceeded by all later blocks of days except Days 3–4 and 25–30 of the postsignal results.

Discussion

Two findings suggest that the large duration increase in Experiment 1 was due to a decrease in expectation of reward rather than to omission of expected reward. First, omission of expected reward had no detectable effect 45–75 s later (Figure 10), the time period that in Experiment 1 showed the largest effect. The standard error of this null result (0.7%) was small enough to easily detect a change of the size seen in Experiment 1 (62% ± 3%). If anything, the effect of reward omission (at the end of the signal) in this experiment should have been larger than in Experiment 1, because

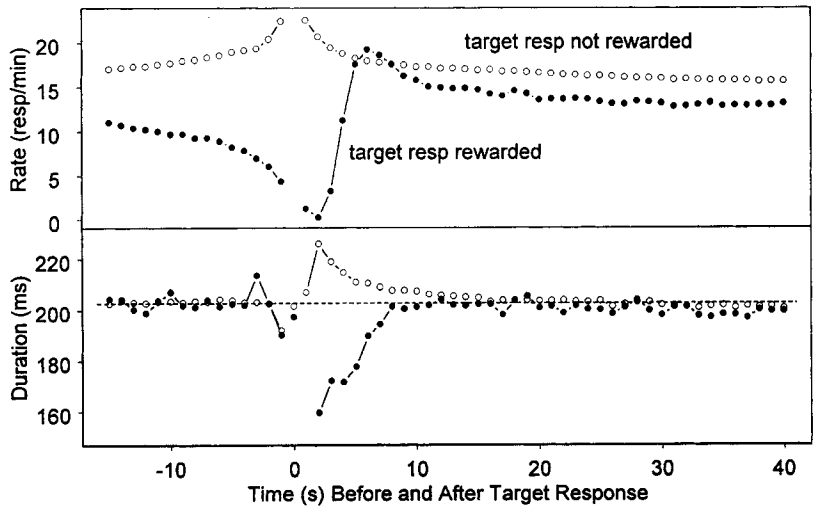

Figure 12. Experiment 2: Response rate (upper panel) and response duration (lower panel) before and after rewarded and unrewarded responses during the intertrial interval. Each point is a 10% trimmed mean over 18 rats. resp = response.

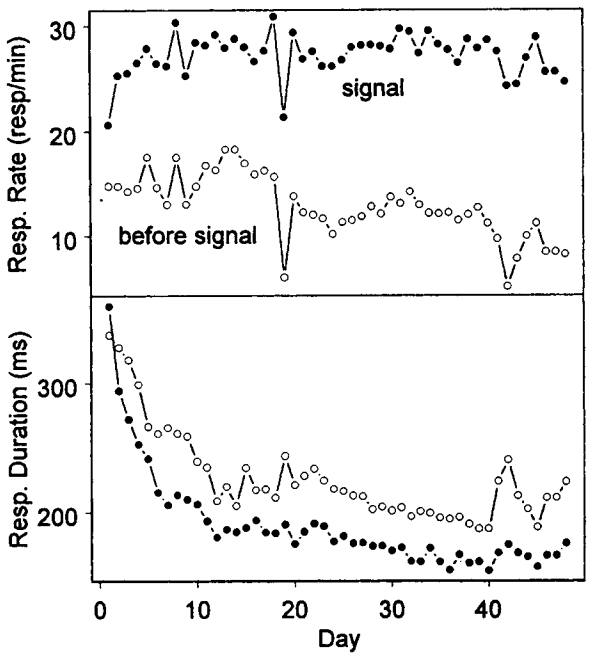

Figure 13. Experiment 2: Response rate (upper panel) and response duration (lower panel) before and during the signal over the course of the experiment. Each point is a 10% trimmed mean over 18 rats. Before signal equals the 29 s before the signal started. Response rates during the signal were based on reciprocals of the latencies of responses. Resp. = response.

the density of food (during the signal) was greater and the probability of reward per response was greater. Second, increasing expectation of reward decreased variation (both panels of Figure 11). The ITI/signal difference (upper panel of Figure 11) was smaller than the effect in Experiment 1 (upper panel of Figure 5), which makes sense, because the change in reward probability was smaller. In Experiment 1, the probability of food after a response went from 80% (assuming the signal was timed with great precision) to zero. The probability of reward during the signal was 80%, but during the ITI it was well above zero (5–10%). The effect of single rewards during the ITI (lower panel of Figure 11) supports the idea that expectations are crucial. When we compare the aftereffects of rewarded and unrewarded responses, we find that there was a significant difference in duration 30–40 s later (during the ITI) when the reward or nonreward event happened during the ITI (Figure 11) but not when it happened at the end of the signal. When food omission occurred at the end of the signal, it presumably changed expectation of food during the signal but had little effect on expectation of food during the ITI.

This experiment provided more evidence that rate and duration are independent (Figures 12, 13, and 14). The selectivity seen in Figure 12 is especially convincing. Not only was the difference in rate (54.0%) much larger than the standard error of the difference in duration (0.7%) but the difference in rate correlated with anything that changed rate, not just one experimental manipulation. During the ITI, many internal states varied, and some of this variation affected response rate. For concreteness, suppose that hunger varied and that increases in hunger increased rate. Because of its effect on rate, hunger will correlate with rate during the ITI. Because of the correlation between rate and probability of reward (upper panel of Figure 12), hunger will correlate with probability of reward. The lower panel of Figure 12 shows, therefore, that variations in hunger large enough to change rate had no detectable effect on duration. Hunger, of course, is just an example; this argument applies to any variation in internal state during the ITI large enough to affect rate. Suppose rate and duration measure different but overlapping portions of the underlying mechanism. If a manipulation that affects the common portion is never used, the overlap will never be discovered. The selectivity shown in Figure 12 implies that if there is a common portion, it is not influenced by anything that varies enough during the ITI to affect rate.

Although the results indicate that the large duration increase after food omission in Experiment 1 was not a frustration effect (because it was not due to reward omission), a smaller frustration-like effect did occur in this experiment. Omission of expected food, both at the end of the signal (Figure 10) and during the ITI (Figure 12), increased duration a small amount. The size, latency, and length of the increase resembled the short-range effect in Experiment 1 suggested by the deviation from linearity in Figure 7.

Animals react in many ways to the omission of expected food (Amsel, 1958, 1992; Carbonaro, Friend, Dellmeier, & Nuti, 1992; LaPlante, 1993; Papini & Dudley, 1997; Prytula, Lawler, & Davis, 1975), so it is not surprising that an effect of omission was observed here. The increase in response duration about 2–9 s after omission of expected food (Figures 7, 10, and 12) had the properties expected of a "frustration" (Amsel & Roussel, 1952, p. 363) effect: (a) It appeared regardless of whether the probability of food decreased after food omission. In Amsel and Roussel's (1952) experiment, the effect—an increase in running speed—occurred after food was omitted in the first goalbox of a double runway. Whether food was omitted in the first goalbox predicted nothing about the probability of food in the second goalbox. (b) It lasted a plausible length of time, about 10 s (Figures 10 and 12). When MacKinnon and Amsel (1964) confined their subjects to the first goalbox for 90 s, the frustration effect disappeared. (c) It was in the

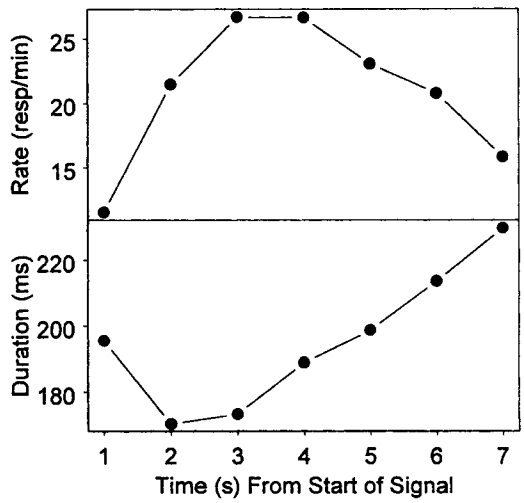

Figure 14. Experiment 2: Response rate (upper panel) and response duration (lower panel) during the signal. Each point is a 10% trimmed mean over 18 rats. resp = response.

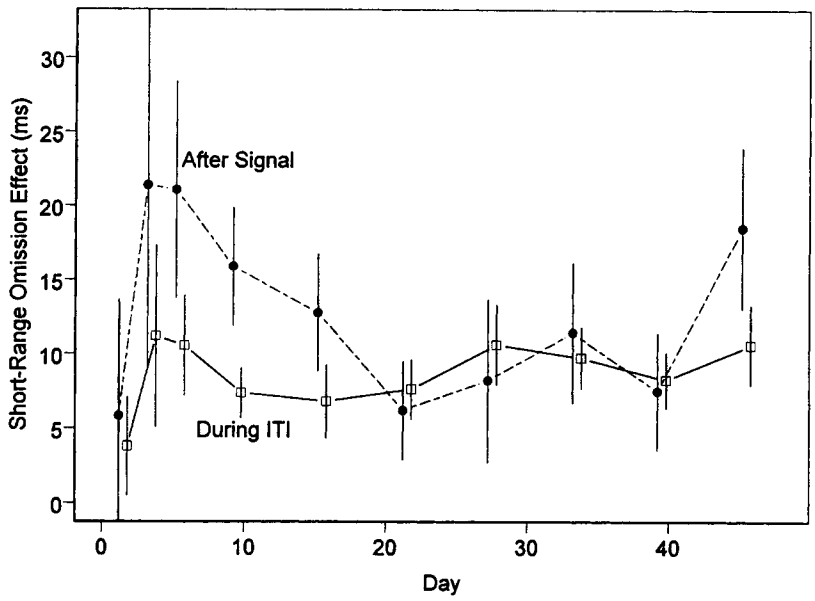

Figure 15. Experiment 2: Effect of reward omission on response duration over the course of the experiment. Each point is a 10% trimmed mean over 18 rats.

right direction. The original effect and the effect observed here involved more energy expenditure because holding down the lever requires force. (d) It required learning. To detect absence requires expectation. Consistent with this, the short-lived duration increase was absent at the start of Experiment 2 (Figure 15).

The effect did not change in size when the probability of reward varied by a factor of 10 (Figures 10 and 12). Such insensitivity to reinforcer probability seems to be unprecedented in an associative response, but it makes sense. Almost all the associative-learning effects that have been studied are anticipatory: They occur before an expected event, and their function is to cause the event, avoid it, or prepare for it (e.g., Hollis, 1997). In contrast, frustration effects occur after something was supposed to happen. Anticipatory behavior needs to vary with the likelihood of the anticipated event, because in most natural situations, the future is uncertain. More than one event must be anticipated, and anticipation of one event can interfere with anticipation of other events. When an event becomes less likely, therefore, it should be anticipated less. In contrast, the best way to react to an event often varies little with the probability of the event. For example, the size of a community's police force should vary with the amount of crime (more crime, more police), but the best way to react to each crime probably depends very little on the amount of crime.

General Discussion

Independence of Rate and Duration

This research began with the idea that rate and duration might be independent because (a) the underlying mechanism can be divided into two parts—one that decides whether to respond and another that implements this decision, and (b) changing the first part should affect rate but not duration, whereas changing the second part should affect duration but not rate. The results support these assumptions. If rate and duration reflected the same process, there would be a one-to-one relation between them—each duration would be associated with only one rate, and vice versa. This was repeatedly found not to be the case. In Experiment 1, plotting duration versus rate made a circle rather than a line (Figure 3). In Experiment 2, uncontrolled variation in rate did not affect duration (Figure 12); rate became constant during training long before duration (Figure 13); and the two measures reached their maximum at different times during the signal (Figure 14). The wide range of independence shown in Figure 3 and the great selectivity shown in Figure 12 are especially strong evidence.

The early evidence for the conclusion that rate and form reflect different processes came from experiments in which a measure of form remained constant in spite of large changes in response rate or probability (Blough, 1978; Corbit & Luschei, 1969; Roberts, 1987). The present evidence is more diverse, more precise (Figure 12), and more balanced. In one case, rate changed and form was constant (Figure 12); in one case, form changed and rate was constant (Figure 13); in other cases, both changed (Figures 3 and 14). It suggests that the initial decision to act is quite vague—maybe something like "press the lever"—to which details of how to press the lever are added downstream.

Precision of Timing

Theories of timing (reviewed by Church, 1989) have interpreted the width of generalization gradients, usually from instrumental responses, as indicators of the precision of a timing system. These results, for reasons spelled out in the *Discussion* of Experiment 1, question that assumption. The rats in Experiment 1 apparently timed the signal more precisely than the width of the response-rate functions (upper panel of Figure 2) would suggest. A few earlier results had hinted at the possibility that animals can time much better than these theories assume. Pavlov (1927, p. 42) reported results from one dog, given a signal for food every 30 min, who

salivated much less if the signal was presented just 1 min early. Roberts (1981) noted that the near symmetry of peak-procedure response-rate functions implied that trial-to-trial variability in timing of the signal was a negligible source of the variability seen in the spread of the functions. Using a model with several parameters, Church and Gibbon (1982, Table 1) estimated a very low coefficient of variation; according to their model, much of the trial-to-trial variability was due to inattention. The precision of timing seen in Experiment 1 may have been due to extensive training; the subjects experienced thousands of trials. With a large amount of practice, Kristofferson (1984) became very accurate at measuring duration.

The conclusion that rats can time quite precisely resolves the puzzle of why rats seem to time much less precisely than humans. Wearden (1992) concluded that coefficients of variation measured from animals (without correction for inattention) were typically twice as large (i.e., discrimination was half as precise) as those measured from humans. There is no obvious evolutionary explanation for such a large difference. If rats have used timing while foraging to decide when to leave a patch (Roberts, 1983), then rats would be expected to measure durations more precisely than humans.

Control of Variation

The conclusions about the precision of timing suggest—generalizing to other stimulus dimensions—that reward increases variability, in the sense that it increases the rate of the rewarded response in similar but easily distinguished situations. Reward "pulls up" a whole generalization gradient that is wider than necessary. This makes functional sense. If one finds food under a tree, one should look for food under similar trees, even if the trees obviously differ (e.g., in location) from the first tree. Businesses follow a similar rule. When a business sells its product, this event, which corresponds to pressing the bar and receiving reward, not only causes that particular business to grow (the economic law of effect); it also stimulates attempts to sell slightly different products (Gomes, 2000). For example, commercial success of one cola drink encourages marketing of other cola drinks with small but clear differences. Because instrumental learning needs variation from which to select but classical conditioning does not, it is reasonable to expect that classically conditioned generalization gradients will usually be narrower than instrumental ones. Pavlov's (1927, p. 42) observation of highly precise timing of a 30-min interval was made with a classically conditioned response.

The results of Experiment 2 suggest—generalizing to other aspects of response form—that variability of the form of responses increases when the expected density of reward decreases. This makes functional sense, because variation has a cost: When some responses are paying off, an increase in the variability of form will decrease the frequency of reward, because some responses will be outside the criteria for reward (e.g., in the case of duration, too short or too long). As the likelihood of reward goes down, there is less to lose, so the cost of variability goes down. If the cost of variability goes down, the optimum amount of variability should rise.

Using response duration to learn about the control of instrumental variability (the variability from which reward selects) makes sense only if variability in duration can serve as a substrate for selection by reward, that is, if subjects can learn to make responses of certain durations. This has been shown several times (e.g., Notterman & Mintz, 1965; Platt, Kuch, & Bitgood, 1973).

The results help explain why extinction increases variability of form (Balsam et al., 1998). They support one of the four explanations mentioned earlier (that expected density of reward is lower during extinction) and argue against the other three. (a) *Lower rate.* The independence of rate and duration (Figures 3, 12, 13, and 14) suggests that changes in rate do not affect duration. (b) *Omission of expected reward.* In Experiment 2, omission of expected reward had no long-lasting effect on duration (Figure 10). (c) *Lower density of reward.* The difference between density of reward and expected density of reward is that the former reflects the recent past (e.g., the last 20 s), whereas the latter is a "best guess" about the near future (e.g., the next 20 s). If a lower density of reward increases variation, variation in Experiment 1 should have increased throughout an empty trial, which is entirely without food. However, the actual pattern of change (Figure 4) was quite different. In Experiment 2, this explanation predicts that response variation should have been greater during the signal than the ITI, because time during the signal is further from the latest reward; the actual result was the opposite (upper panel of Figure 11).

The study of variability, once popular (e.g., Gengerelli, 1928; Guthrie & Horton, 1946; Kuo, 1922; Skinner, 1938), seems to be undergoing a revival (Balsam et al., 1998; Neuringer, Deiss, & Olson, 2000), to which the study of response duration may contribute. The results of this study show the value of distinguishing between (a) variation in the situations that elicit a response (increased by reward) and (b) variation in response form (decreased by reward).

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