



High-rate operant behavior in two mouse strains: A response-bout analysis

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ABSTRACT

Operant behavior sometimes occurs in bouts characterized by an initiation rate, within-bout response rate, and bout length. The generality of this structure was tested using high-rate nose-poking in mice. Reinforcement of short interresponse times produced high response rates while a random-interval schedule held reinforcement rates constant. BALB/c mice produced bouts that were more frequent, longer, and contained a higher within-bout rate of responding (nine nose-pokes/s) than did the C57BL/6 mice (five nose-pokes/s). Adding a running wheel decreased total nose-pokes and bout length, and increased bout-initiation rate. Free-feeding reduced nose-poking by decreasing bout-initiation rate. Photoperiod reversal decreased bout-initiation rate but not total nose-poke rate. Despite strain differences in bout structure, both strains responded similarly to the interventions. The three bout measures were correlated with overall rate but not with each other. Log-survival analyses provided independent descriptors of the structure of high-rate responding in these two strains.

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1. Introduction

Operant behavior sometimes occurs in bouts characterized by three parameters: bout-initiation rate, within-bout response rate, and bout length (Shull et al., 2001, 2004). Bout-initiation rate is influenced by motivational variables like reinforcement rate and deprivation (Shull et al., 2001, 2004). Bout length is increased by adding a tandem variable ratio (VR) requirement to a variable interval (VI) schedule, a contingency that results in long runs of responding. Within-bout response rate is affected by variables that influence motor function or the physical characteristics of responding, like the type of response device (Shull et al., 2001, 2004; Shull and Grimes, 2003).

A statistical model based on an analysis of the frequency distribution of interresponse times (IRTs) has been introduced to estimate these three parameters (Shull et al., 2001). The model has been applied to the behavior of rats and pigeons under single schedules of reinforcement and to pigeon behavior under concurrent schedules (Shull et al., 2001; Bennett et al., 2007; Davison, 2004). This model worked well with rat behavior but pigeon behavior has produced a challenge, a species difference that could be due to methodological conventions: overall reinforcement rates greater than 10 h^{-1} results in clearly defined response bouts for rats but not pigeons, apparently because of species differences in engagement in activities other than lever-pressing or key-pecking in most operant chambers (Shull, 2005).

Behaviorally divergent strains like C57BL/6 and BALB/c mice provide an excellent template for further testing of the applicability of this model. As compared with BALB/c mice, C57BL/6 mice show higher levels of spontaneous locomotor activity, spend more time in the center of open arenas and more time in the arms of an elevated plus maze (Crawley et al., 1997; Tang et al., 2005; Beuzen and Belzung, 1995). The last two are interpreted as diminished anxiety in C57BL/6 mice but in the present context all three also might be interpreted as alternative behavior. In contrast, BALB/c mice show higher baseline response rates than C57BL/6 in operant tasks (Wang and Fowler, 1999; Heyser et al., 1997), and BALB/c mice lick a force plate with greater force and faster pace than C57BL/6 mice (Wang and Fowler, 1999).

These two strains show strong circadian patterns in locomotor activity (Kopp et al., 1998; Kopp, 2001) and ambient illumination may have differential effects on these strains. Pigmented C57BL/6 mice, for example, spend significantly more time in the illuminated portion of a chamber than albino BALB/c mice (Griebel et al., 2000).

High-rate operant behavior was used in the present studies, in part because of an interest in using such responding to identify motor deficits associated with drug or toxicant exposures but also because it presents some interesting tests of the log-survivor model. With many procedures that generate high-rate behavior, it can be difficult to separate motor from motivational influences over behavior (Newland, 1995). The log-survival analysis (Shull et al., 2001) offers just such a separation if these two influences act independently. Conditions that generate high-rate behavior often impose a direct relationship between responding and reinforcement rate. Accordingly, exposures or other treatments that impair responding

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also lower reinforcement rate, which may further reduce response rate, resulting in a downward spiral that blurs motivational and motor influences. The independence of motivational and motor determinants is important in the model because otherwise the parameters obtained from log-survival analyses will not provide independent information about response structure.

The challenge, then, lies in maintaining a stable reinforcement rate while dissociating the relationship between response rate and reinforcement rate. The solution is the percentile schedule of reinforcement applied to the IRT and a time-based reinforcement schedule that is applied to criterion IRTs. In the implementation described below, to be eligible for reinforcement, an IRT had to be shorter than 50% of the previous 10 IRTs. By selectively reinforcing short IRTs, this percentile schedule generates high response rates (i.e., short IRTs) while continuously adjusting the IRT criterion according to an individual animal's most recent performance. This adjustment prevents behavior from undergoing extinction if responding becomes impaired. Criterion IRTs are reinforced under a random-interval (RI) 60 s schedule, so reinforcement rate is held constant unless response rate becomes very low.

The present study included two manipulations hypothesized to influence bout-initiation rate. First, a running wheel was added to the experimental chamber. We predicted that running would compete with nose-poking for sucrose, but it was not clear whether this influence would appear in bout length, bout-initiation rate, or both. Second, food restriction was eliminated. We predicted this would lower overall response rate, primarily by reducing bout-initiation rate without affecting the other parameters (cf. Shull, 2004). Two additional questions were addressed by comparing two mouse strains. As noted earlier, BALB/c mice lick more vigorously in an operant licking task than C57BL/6 mice. We were interested in whether this strain difference would appear in within-bout response rate, hypothesized to reflect motor capabilities independently of other manipulations (Shull et al., 2001). Finally, also noted above, these strains' behavior is strongly influenced by photoperiod and could be differentially affected by ambient illumination, so we examined the role of photoperiod in the structure of response bouts in the mice.

2. Materials and methods

2.1. Subjects

Subjects were four BALB/c and seven C57BL/6 mice with no previous experimentation history. Mice were housed individually in a room with 12-h light/dark cycles in an AAALAC-accredited facility. For most conditions the animals were maintained on a reverse light–dark cycle (lights off at 6:00 a.m.) and 85% free-feeding weight. They were allowed free access to water at all times excluding experimental sessions. All experiments were approved by the Auburn University Animal Care and Use Committee.

2.2. Apparatus

Four MedPC (St. Albans, VT) rat operant chambers fitted to accommodate mice were situated inside sound-attenuating ventilated shells. Each chamber contained a nose-poke device (model no. ENV-313M) located in a recessed space on the front wall to the left of the food tray. A lever, unused here, was on the right. Mice activated the nose-poke device by interrupting a photobeam with their snouts. For some sessions, a 7-in. diameter running wheel was added at the back of the operant chamber that recorded 1/4 wheel revolutions. LED signal lights were located above both the nose-poke device and the lever. A houselight was near the top of the chamber directly above the food tray. A pellet dispenser delivered

20 mg sucrose pellets into a food tray. MEDPC was used to program the experiment and collect data with 0.01 s resolution.

2.3. Procedure

Nose-poking for sucrose pellets was autoshaped in an overnight session. A trial started by lighting the LED over the nose-poke device for 30 s. Coincident with the termination of this interval, a 0.1 s 4500 Hz sonalert tone sounded and a sucrose pellet was delivered. Then, the chamber was darkened for a 5-min intertrial interval. Every elicited nose-poke immediately initiated a reinforcer delivery. After 10 reinforced responses, the LED over the nose-poke was lit constantly, the autoshaping procedure ended, and nose-poking was reinforced under a fixed ratio (FR) 1 schedule. The sessions ended after the earlier of 12 h or 100 pellets delivered.

The subsequent contingencies can be described as a second-order random-interval t_s (Percentile 10:0.5 S^P) schedule of reinforcement. After an average of t_s , a criterion response was reinforced with a sucrose pellet. The random-interval (RI) parameter, t , began at 1 s and gradually increased to 60 s. Criterion responses were identified with the unit schedule, a percentile 10:0.5 schedule. When a nose-poke occurred, the IRT that it terminated was compared with the previous 10 IRTs (the look-back window). If the current IRT was shorter than 50% of the previous 10, then it produced a 0.05-s tone and was eligible for reinforcement. The S^P designation indicates that the brief tone was paired with reinforcement. Thus, to qualify for reinforcement the animal had to respond faster than it did on half of its previous responses. For example, if the animal's previous IRTs were (after sorting) 1.2 s, 1.2 s, 1.0 s, 0.9 s, 0.8 s, 0.8 s, 0.6 s, 0.5 s, 0.4 s, and 0.3 s, then any IRT less than 0.8 s would be eligible for reinforcement. All sessions lasted 30 min and occurred 5 days a week. Subjects were exposed to three different phases. Each phase was preceded by a baseline. The phase-specific intervention was imposed after five consecutive sessions with no systematic variation in overall nose-poke rates and, when relevant, running rate in the wheel.

2.3.1. Phase 1: running wheel added

After baseline stabilized, a running wheel was introduced and the three bout parameters were estimated for this condition. The mean from the last three sessions was used for data analysis.

2.3.2. Phase 2: free-feed

The wheel was removed and baseline responding was reestablished. Then, the mice were provided unrestricted access to standard rodent chow in their home cages for 10 days. Response rates at the end of this free-feeding phase were low, so IRTs from the last four sessions were concatenated before conducting the log-survival analysis.

2.3.3. Phase 3: photoperiod reversal

Animals were returned to 85% of free-feeding weight, and the baseline responding was reestablished. Food restriction remained in place and the photoperiod was reversed on a Friday such that lights turned on at 6:00 a.m. Experimental sessions commenced again on the following Tuesday, but this time during the less active (light) photoperiod. The last three sessions were used for data analysis.

2.4. Data analysis

A log-survival analysis was employed to differentiate between bout initiations and within-bout responses (Shull et al., 2001, 2004). All but the longest 2% of the interresponse times from a session were sorted from shortest (representing high response rates) to

longest and plotted as a survival function. Post-reinforcer pauses were omitted.

$$Y(t) = (1 - p)e^{-wt} + pe^{-bt} \tag{1}$$

A two-exponential function developed by Shull et al. (2001) (Eq. (1)) was fitted to this survival function of IRTs using nonlinear least squares with reciprocal *Y* weighting to estimate bout-initiation rate (*b*), within-bout response rate (*w*), and bout length (*1/p*). The *Y(t)* term represents the proportion of IRTs > *t*; *p* is the proportion of responses that initiate a bout, and (1 - *p*) is the proportion of responses that are within a bout. Because it resulted in better fits, the regression was conducted after taking the log₁₀ of each side (i.e., log₁₀(*Y*) = log₁₀[(1 - *p*)e^{-*wt*} + *pe*^{-*bt*}]). RS/1 software (Brooks Automation, Chelmsford, MA) was used for data management and to perform the nonlinear regressions required to estimate the bout parameters.

Mixed ANOVA was used for inferential statistics unless otherwise stated. ‘Strain’ was a between-subject variable and ‘intervention’ was a within-subject variable. To evaluate the independence of the parameters, intercorrelations were computed using Pearson-product moment correlations among parameter estimates from all conditions, carried out with both strains combined and for each strain alone. Statistical significance was assessed at an alpha level of 0.05, and *p*-values greater than 0.1 are not reported. All statistical analyses included all cases unless otherwise specified.

3. Results

Response rates varied over a 9.5-fold range across strains and conditions (Table 1). Reinforcement rate varied little across phases except in the free-feeding condition for C57BL/6 mice. Reinforcement rate was higher for BALB/c mice across conditions (from reinforcement rates in Table 1, as shown by an independent samples *t*-test, *t*(6) = 3.137, *p* = .01).

3.1. Phase 1: running wheel added

Fig. 1 shows the results from the running-wheel phase, with separate panels for total nose-pokes and the three bout parameters. The BALB/c mice nose-poked at a higher rate than the C57BL/6 mice, *F*(1, 9) = 8.24, *p* = .018. For both strains, nose-poking occurred at a lower rate when the wheel was available, *F*(1, 9) = 10.17, *p* = .013. There was no significant wheel × strain interaction for nose-poking. One outlier (Mouse 106) was more than two standard deviations above the mean and removed before conducting the ANOVA. C57BL/6 mice ran significantly farther per session (*M* = 227 m) than did BALB/c mice (*M* = 174 m), as shown by an independent *t*-test, *t*(9) = -2.608, *p* = .028.

BALB/c mice had higher bout-initiation rates than the C57BL/6 mice, *F*(1, 9) = 8.65, *p* = .016, and these rates were higher when the wheel was present, *F*(1, 9) = 17.7, *p* = .002, than when absent for both strains. There was not a significant wheel × strain interac-

tion for bout-initiation rate. From the bout-initiation rates of about 0.25–0.5 s⁻¹, we estimate that wheel running occurred in bouts of about 2–4 s, depending on strain.

BALB/c mice had higher within-bout response rates than the C57BL/6 mice, *F*(1, 9) = 12.71, *p* = .006, but the wheel did not alter within-bout response rates for either strain. Adding the wheel decreased bout lengths for both strains by *F*(1, 9) = 26.88, *p* = .001, but there was no strain difference or interaction on this measure. Overall, adding the running-wheel resulted in shorter, more frequent bouts.

3.2. Phase 2: free-feed

The results from the free-feeding phase are shown in Fig. 2. Again, BALB/c mice produced significantly more nose-pokes than C57BL/6 mice, *F*(1, 9) = 59.55, *p* < .001. Fewer nose-pokes occurred during the free-feeding condition for both strains, *F*(1, 9) = 32.89, *p* < .001. There was no interaction between strain and condition.

BALB/c mice initiated more bouts than C57BL/6 mice, *F*(1, 9) = 42.2, *p* < .001, and more bouts were initiated when mice were food restricted than when mice were free-fed, *F*(1, 9) = 52.07, *p* < .001. There was not a significant interaction between strain and deprivation condition.

Within-bout response rate was higher for BALB/c mice, *F*(1, 9) = 8.17, *p* = .019. Feeding condition did not affect within-bout response rate (*p*'s > .1). The *p*-values for a main effect of feeding condition, strain, and their interaction were all between 0.06 and 0.09. Visual inspection suggests that bout length did decline during the free-feeding condition for C57BL/6 mice, and a post hoc paired samples *t*-test indicated that bout length was significantly shorter for C57BL/6 mice during the free-feeding phase *t*(6) = 3.506, *p* = .013, but not for the BALB/c mice. Overall, free-feeding reduced total nose-pokes, bout-initiation rate, but not within-bout rate or bout length for BALB/c mice. Effects on bout length are suggestive (for C57BL/6 mice only).

3.3. Phase 3: photoperiod reversal

Reversing the photoperiod did not affect nose-poke rate, but a higher bout-initiation rate occurred during dark sessions (*M* = 0.224 bouts/s) than light sessions (*M* = 0.157 bouts/s) for both strains, *F*(1, 8) = 16.50, *p* = .004. No interaction of photoperiod and strain was detected for bout length or within-bout response rate. As previously, the within-bout rate was higher for the BALB/c mice *F*(1, 8) = 6.52, *p* = .034. One BALB/c mouse died during the third phase and was excluded from the analysis of this phase.

3.4. Correlations

Total nose-pokes were correlated with bout length, within-bout rate, and bout-initiation rate for both BALB/c and C57BL/6 mice (pairwise correlations ranged from +0.29 to +0.58). The correlations among bout-initiation rate, within-bout response rate and

Table 1
Total nose-pokes and reinforcers earned per session.

Condition	Sessions	BALB/c			C57BL/6		
		Total nose-pokes ^a	S.D.	Reinforcers earned ^a	Total nose-pokes ^a	S.D.	Reinforcers earned ^a
Baseline 1	12	2186	302	27.5	1078	875	23
Wheel	13	1721	1193	28.4	595	403	22.8
Baseline 2	10	3249	675	29.7	1035	367	24.7
Free-feeding	9	2064	505	24.8	341	168	13
Baseline 3	12	2322	663	24.7	871	669	22.6
Reverse photoperiod	15	2091	536	28.6	685	561	21.7

^a The average of the last three sessions for all animals.

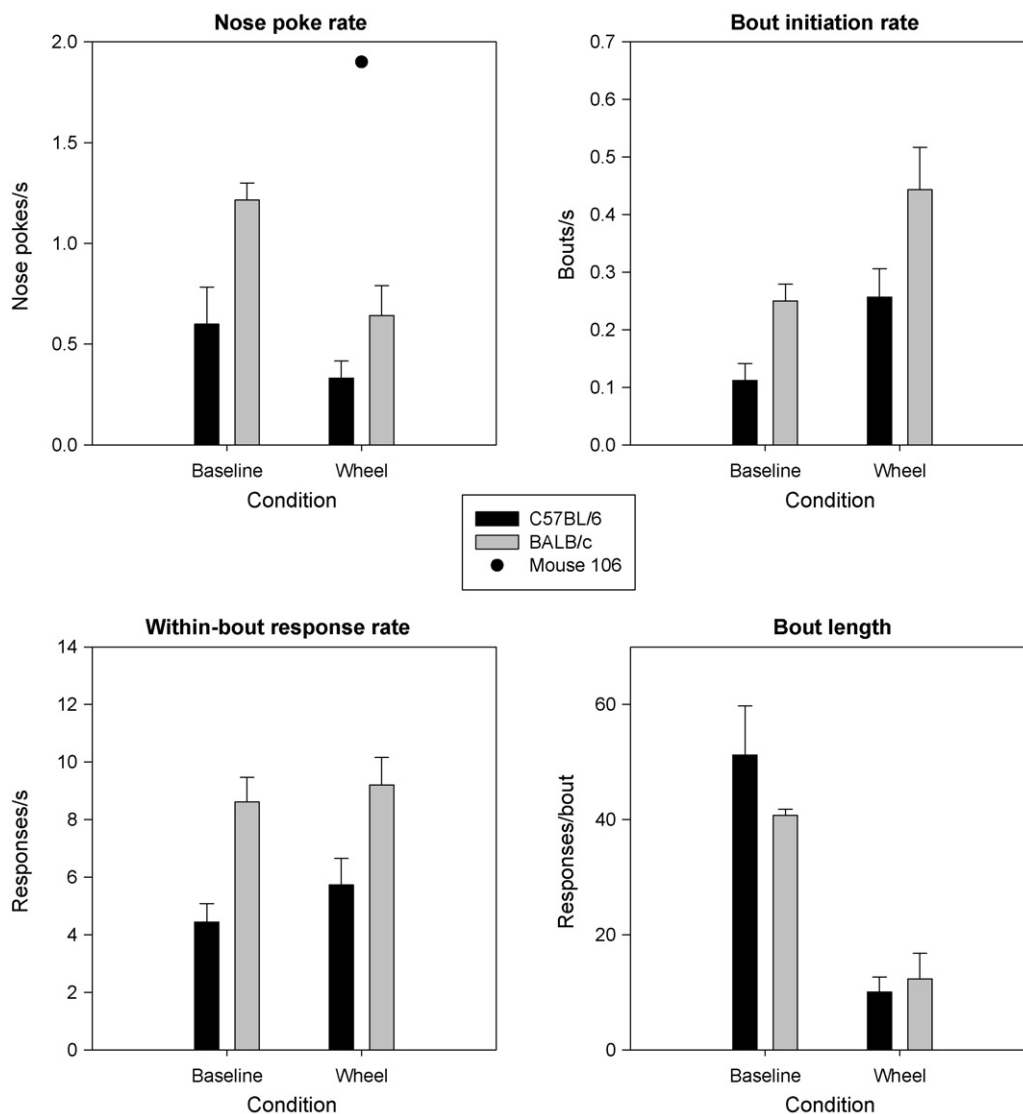


Fig. 1. The effect of adding a wheel in the experimental chamber on (clockwise from top left) nose-poke rate, bout-initiation rate, bout length, and within-bout response rate. All rates are in units of rs/s. Black and gray bars represent C57BL/6 and BALB/c mice, respectively. Error bars show the standard error of the mean. Total nose-pokes for an outlier (Mouse 106) are shown separately.

bout length, however, were all statistically indistinguishable from 0.

3.5. Representative sessions

Fig. 3 contains representative log-survival plots (left panels) to illustrate the “broken-stick” appearance that occurs in these plots. The line shows the fit of Eq. (1) to the IRTs. For example, the equation for BALB/c Mouse 103 baseline is $Y = 0.96e^{-12.1x} + 0.04e^{-0.26x}$, representing within-bout and bout-initiation rates of 12.1 nose-pokes/s and 0.26 bouts/s, respectively. Bout lengths were $1/0.04 = 25$ responses/bout. Inserting the wheel produced within-bout rates, bout-initiation rates, and bout lengths of 12.8 nose-pokes/s, 0.62 bouts/s, and $1/0.09 = 11.1$ nose-pokes/bout, respectively. The wheel resulted in a faster bout-initiation rate, indicated by a steeper slope on the right leg, but no change in the within-bout rate (left leg).

We did not use R^2 as a marker of the quality of the fits because only pseudo R^2 can be calculated for nonlinear regression and its interpretation is sometimes questionable. Instead, we used the coefficient of estimate for each parameter. The coefficient of estimate is the standard error of the estimate divided by the mean;

a low number indicates a precise parameter estimate. We compared the coefficient of estimate for each parameter illustrated in Fig. 3 with the coefficient of estimate for the all fits on a strain-by-strain basis (i.e., BALB/c against all BALB/cs' and C57BL/6 against all C57BL/6s'). Of the 12 parameter estimates illustrated in Fig. 3, 2 were better than 25%, 5 were between 25% and 75%, and 5 were worse than 75% of all fits. These, then, were not best cases but rather could be described as characteristic of good or adequate fits. The median coefficient of estimate across all fits (all parameters, all mice) was 0.0033 and the worst coefficient of estimate was 0.105, so the precision of the parameter estimates can be described as excellent to adequate.

Cumulative records (right) show the course of responding through the same sessions for the two strains. BALB/c mice (top two rows) produced more nose-pokes than C57BL/6 mice (bottom two rows). Adding the wheel produced a more ragged shape to the cumulative record because it resulted in shorter but more frequent bouts of nose-poking. Bouts might be more easily visualized in the event record under each cumulative record. Note that nose-poking, but not wheel-running, declined toward the end of the session for C57BL/6 mice. We did not examine this systematically, but can com-

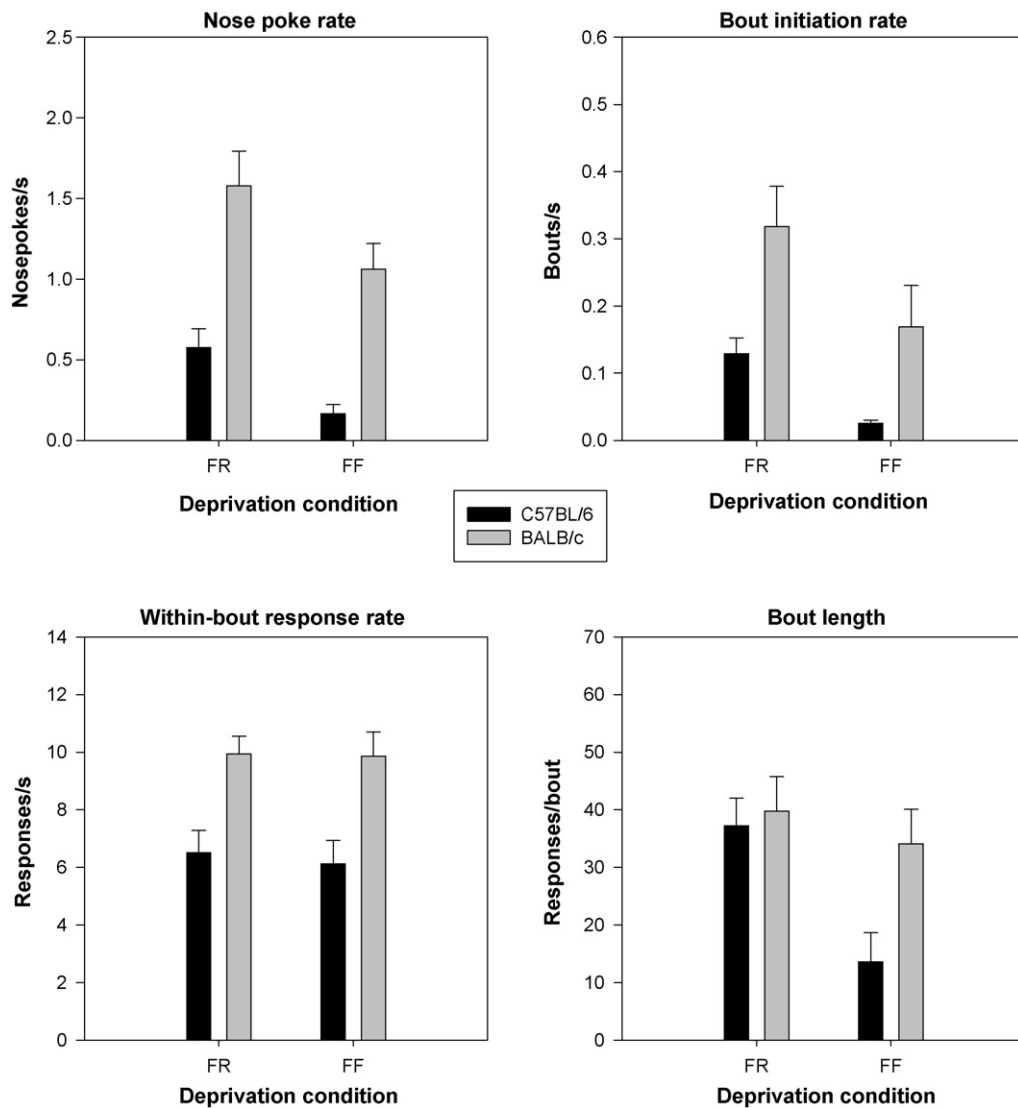


Fig. 2. The effect of food deprivation on total nose-pokes and the three bout parameters, structured as in Fig. 1.

ment that this end-of-session decline was observed frequently in the C57BL/6 mice.

4. Discussion

The present experiment supports two broad conclusions about high-rate nose-poking in these mouse strains: overall rates of nose-poking differed between the two strains, and the interventions altered bout structure similarly in the two strains. Total nose-pokes were 2–3 times higher for BALB/c mice than for C57BL/6 mice, and this was due both to higher bout-initiation rates and higher within-bout rates. Bout-initiation rates were about 2–4 times higher for BALB/c mice than for C57BL/6 mice. Within bouts, BALB/c mice nose-poked over 8 responses/s and the C57BL/6's did so at about 4–6 responses/s. By comparison, the within-bout rates for rats pressing a disk and lever-pressing are about 3–5 responses/s (Shull et al., 2004) and 0.7–1.2 responses/s (Shull and Grimes, 2003), respectively. These within-bout rates likely reflect motor differences across strains and species, the operation of different response devices, and reinforcement contingencies. Bout lengths were usually similar between the two strains.

Despite strain differences in baseline behavior, C57BL/6 and BALB/c mice responded similarly to most interventions. For exam-

ple, the presence of a running wheel, which can be viewed as an alternative reinforcer (Dunham, 1977; Belke and Belliveau, 2001), decreased overall nose-poking and, for each strain, the decrease was due to a sharp, four to fivefold reduction of bout length. This decrease was accompanied by an increased bout-initiation rate which, as suggested by inspection of log-survival plots from individual animals (Fig. 3), may be related to the elimination of very long pauses when the wheel was present. In short, when the wheel was available, the nose-poke bouts were shorter, more frequent, and perhaps accompanied by fewer long pauses. Free-feeding affected the structure of response bouts differently. Non-deprived animals initiated bouts at a lower rate, but bout lengths were affected only in the low-rate C57BL/6 mice. Neither adding a running-wheel nor food satiation affected within-bout rates.

The different effects of satiation and adding a running-wheel can be understood if reinforced nose-poking is viewed as a choice between two alternatives: the explicitly reinforced response (nose-poking) and doing something else such as grooming, exploring, or, when possible, running in a wheel (Hinson and Staddon, 1978). Seen this way, a concurrent schedule is present and the mouse switches between two activities such that the time devoted to one alternative is related to its relative value (Baum and Rachlin, 1969; Herrnstein, 1970). Under concurrent schedules, the rate of switching is highest

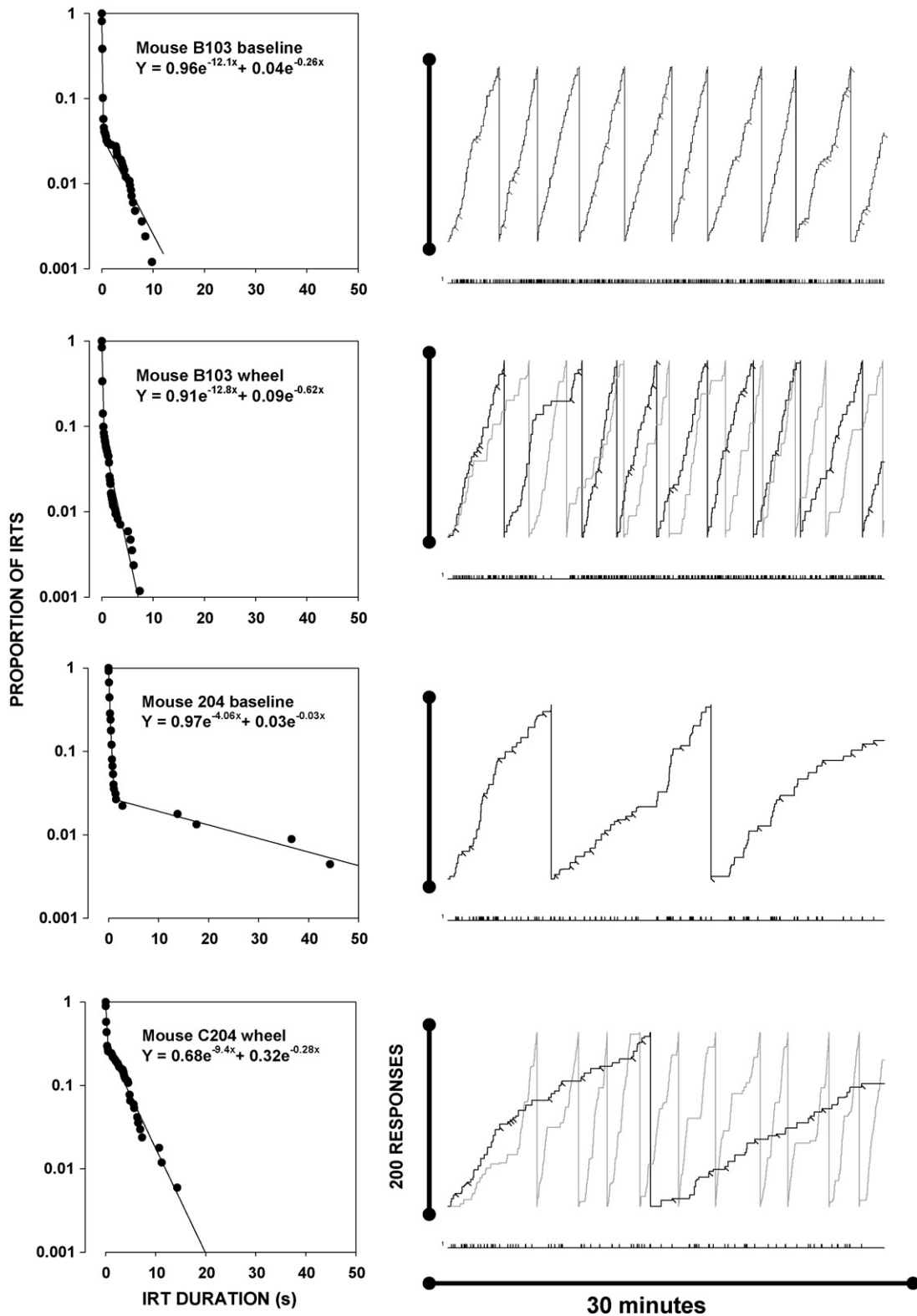


Fig. 3. Log-survival plots (left column) illustrate representative sessions with and without the running-wheel for BALB/c (top two rows) and C57BL/6 mice (bottom two rows). A point on the plot shows the proportion of IRTs that are longer than the value on the X-axis. For example, all the IRTs are longer than the shortest, left-most point. The fitted line resembles a broken-stick with two legs. The equation for the fitted line is shown in the figure. Cumulative records (right side) show nose-poking (black line) and wheel running (gray line) through the course of the sessions represented in the log-survival plots. Each row represents a single session. Each criterion nose-poke advanced the black pen upward. Reinforcers are indicated by diagonal marks. The inter-bout intervals may be easier to see in the event records immediately under the cumulative records. Each vertical line on the event record represents a nose-poke and gaps show inter-bout intervals.

when two alternatives are reinforced at equal rates, or are equally valued (Alsop and Elliffe, 1988; Myerson and Hale, 1988; Newland et al., 2004). Switching decreases as preference for one alternative increases. Bout-initiation rate might be viewed as the rate of switching to nose-poking, and bout length as the rate of switching out of nose-poking (Shull et al., 2001). These two parameters, therefore, may indicate how food satiation or the availability of a wheel changed the relative value of nose-poking.

The short bout lengths and high bout-initiation rates engendered by the running-wheel suggest that switching occurred at a high rate. Accordingly, running for a caged mouse may be nearly as valued as sucrose for that food-deprived mouse. By comparison, food satiation decreased bout-initiation rate, rate of switching into a bout of nose-poking, for both strains, suggesting that preference shifted away from nose-poking. That is, free-feeding increased the relative value of other behavior. Free-feeding may also have decreased bout length but this effect was less pronounced than that seen with the addition of the running wheel.

Support for this analysis can be found in a recent paper by Belke and Pierce (2009). In that study, rats chose between running in a wheel and consuming sucrose under different conditions of food satiation and deprivation. Choices were expressed by lever-pressing under different response requirements. Decreasing the animals' body weight shifted preference toward sucrose. Moreover, the appendix describes changeover rates and time spent lever-pressing for sucrose or wheel reinforcement. We examined the ratio of time spent responding for food to that for wheel running. As this ratio approached 1.0 (indifference) the number of changeovers increased over conditions where there was a clearly expressed preference for one or the other reinforcer.

Within-bout rates also showed substantial strain differences, but since this variable was not affected by interventions that influenced the other two parameters it likely reflected different behavioral characteristics. Thus, BALB/c mice produced bouts and response rates within these bouts higher than those seen in the C57BL/6. This pattern is reminiscent of strain differences in motor behavior observed by Wang and Fowler (1999) in which BALB/c mice licked more vigorously and in higher-rate response bouts than C57BL/6 mice.

Bout-initiation rates were higher during the dark cycle, when mice are typically more active and when they tend to feed (Kopp et al., 1998; Kopp, 2001), than during the light cycle. Even so, no statistically significant difference in overall nose-poking appeared, and the other bout parameters were unaffected as well. As noted earlier, the bout-initiation rate is influenced by long IRTs so this increased initiation rate may indicate that there are fewer long pauses between bouts during the dark cycle. The rate of responding within a bout and the length of the bout are unaffected by photoperiod. This suggests that the partitioning of behavior using log-survival analysis might be able to detect subtle differences in response patterns that are missed by a global measure such as overall response rate.

Shull et al. (2001) argued that within-bout response rate and bout-initiation rate reflect different influences over responding, implying that they should be correlated with overall response rate but uncorrelated with one another. That prediction was supported here. The availability of running-wheel influenced the bout structure of nose-poking differently than did food restriction, and within-bout rate was affected only by strain. However, changes in bout parameters across conditions were correlated with overall nose-poke rate.

Finally, the second-order RI 60s (percentile 10:0.5 S^P) schedule was examined as a tactic for generating high response rates

while holding reinforcement rates constant. Changes in reinforcement rate across conditions were inconsequential and largely due to strain differences over as much as a fivefold change in response rate (595–3249 nose-pokes/sessions). Only after nose-poke rates dropped to 341/session, about 11 min^{-1} , did reinforcement rates decline.

In sum, the two mouse strains show distinct patterns in operant responding that can be described using log-survival analyses. Strain differences were seen in bout structure but not in the sensitivity of this structure to the interventions imposed here. The bout parameters reflect different influences over responding, were uncorrelated with one another, and were influenced differently by food satiation, the addition of a running wheel, strain, and photoperiod reversal.

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