A Test of the Aversive Transition Account: Extended Pausing Following Signaled
Rich-Lean Transitions on Multiple Fixed-Ratio Schedules in Fischer 344 and Lewis
Rats

By

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Abstract

On multiple schedules ending in two different magnitudes of reinforcement, a signaled transition from a preceding large (rich) to an upcoming small (lean) reinforcer occasions long post-reinforcer pauses compared to transitions from lean to rich, or when magnitude is constant (e.g., rich-rich and lean-lean transitions). A behavioral process that may underlie extended pausing at signaled rich-lean transitions is that these transitions are aversive and set the occasion for escape in the form of extended pausing. The present study evaluated this hypothesis by examining pausing at signaled rich-lean transitions in two inbred strains of rats putatively differing in sensitivity to aversive stimulation. Fischer 344 rats are more sensitive to aversive stimuli and so should pause longer than Lewis rats at the signaled transition from large to small reinforcers. Pausing was assessed at four different signaled transitions (rich-lean, rich-rich, lean-rich, and lean-lean) across a range of fixed-ratio values (1, 25, 50, 75, and 100). Consistent with the aversive transition hypothesis, Fischer 344 rats paused longer than Lewis rats at signaled rich-lean transitions at most ratio values. Control procedures suggest this difference is not due to motoric differences between rat strains.

A fixed-ratio (FR) schedule delivers a reinforcer after n responses, where n is the size of the ratio (Ferster & Skinner, 1957). Responding on FR schedules is characterized by a "break-and-run" pattern composed of a period of nonresponding (a break, or pause) after each reinforcer followed by a relatively high rate of responding (a run) until the next reinforcer is delivered. The period of nonresponding often exceeds the time required to consume the reinforcer. Pausing under FR schedules could be considered maladaptive because it delays the delivery of the next reinforcer (e.g., Lattal, 1991). A host of variables affect pause duration on FR schedules, such as the size of the ratio (Felton & Lyon, 1966; Powell, 1968), effort required to complete each response (Alling & Poling, 1995), the probability of reinforcement (Crossman, 1968; McMilan, 1971), the level of deprivation (Malott, 1966), and reinforcer magnitude (Lowe, Davey, & Harzem, 1974; Powell, 1969).

The effects of reinforcement magnitude on pausing are less clear (Harzem, Lowe, & Davey, 1975; Inman & Cheney, 1974; Lowe et al. 1974; Perone, Perone, & Baron, 1987). Some evidence suggests that large reinforcers produced long pause durations (e.g., Lowe et al.), where other studies have found the opposite (e.g., Inman & Cheney). As a result, researchers have debated whether pausing is controlled by the past reinforcement conditions or by the stimuli correlated with the upcoming reinforcement conditions (e.g., Griffiths & Thompson, 1973; Harzem & Harzem, 1981). Harzem and Harzem argued that pausing is controlled by the past reinforcer—a post-reinforcement pause (Ferster & Skinner, 1957). Applied to the effects of reinforcer magnitude, this account holds that long pauses should follow large

reinforcers and short pauses should follow small ones. Consistent with this, when Lowe et al. exposed rats to FR schedules ending in different concentrations of sweetened condensed milk (i.e., 10% to 70%) that varied unpredictably across trial blocks (a mixed schedule) pausing duration was directly related to the past reinforcer magnitude.

Proposing a different account of pausing, Shull (1979) suggested that pausing is controlled by upcoming discriminable reinforcement conditions—a pre-ratio pause (Griffiths & Thompson, 1973). According to this account, signaling an increase in reinforcer magnitude will decrease pausing whereas signaling a decrease in magnitude should increase pausing. Inman and Cheney (1974) exposed rabbits to a two-component multiple schedule. The components were FR schedules and had the same response requirement but were associated with distinct stimuli (i.e., different colored stimulus lights) that signaled the delivery of large or small amounts of water. In support of the pre-ratio pausing account, pauses were shorter to prior to large reinforcers than before small ones, when rabbits were exposed to FR schedules that signaled large amounts of water.

Perone et al. (1987) proposed that inconsistencies between Inman and Cheney's (1974) and Lowe et al.'s (1974) results were due to procedural differences (the use of either mixed or multiple schedules) and that both accounts of the determinants of pausing were correct. Specifically, in a mixed schedule, pausing can only be controlled by the past reinforcer magnitude because the upcoming reinforcer magnitude is not signaled by discriminative stimuli. Alternatively, under multiple

schedules pausing may be controlled by *both* the past (i.e., the amount just obtained) and signaled upcoming reinforcement magnitude (e.g., key colors correlated with specific amounts of food), thereby supporting both the pre-ratio (Inman & Cheney) and post-reinforcement (Lowe et al.) accounts of pausing under ratio schedules of reinforcement.

To test this hypothesis, Perone and Courtney (1992) exposed pigeons to both mixed and multiple (e.g., FR 80-FR 80) schedule conditions in which schedule components randomly alternated within session between different amounts of food. In the multiple-schedule condition, distinct stimuli (i.e., different key colors) signaled the delivery of either a small (1-s access to grain) or large (7-s access to grain) amount of food following the completion of the ratio requirement. During signaled transitions from rich (large reinforcer amount) to lean (small reinforcer amount) schedule components, longer pause durations were observed (approximately 35 s) relative to the other transition types (less than 5 s at rich-rich, lean-lean, and lean-rich transitions). When the multiple-schedule-correlated stimuli were removed (a mixed schedule), pauses were unaffected by the upcoming reinforcer amount, but were longer after rich than lean reinforcers. Under the mixed schedule, pausing never approximated that observed at rich-lean transitions in the multiple-schedule condition.

Extended pausing at signaled rich-lean transitions is due neither to increased consumption time nor momentary satiation because long pauses are not observed at rich-rich transitions, nor is it due to the signaled upcoming lean reinforcer because long pauses are not observed at lean-lean transitions. Rather, extended pausing at

signaled rich-lean transitions is under the joint control of past and signaled upcoming schedule conditions (e.g., Harzem & Harzem, 1981; Shull, 1979). Extended pausing at signaled rich-lean transitions is a robust finding observed across species (rats: Baron, Mikorski, & Schlund, 1992; pigeons: Perone, 2003; Perone & Courtney, 1992; monkeys: Galuska, Wade-Galuska, Woods, & Winger, 2007; humans with intellectual disabilities: Bejarano, Williams, & Perone, 2003; Williams, Saunders, & Perone, in press), responses (e.g., levers, keys, and touch-screens), and reinforcers (e.g., food, points, money, and drugs). In addition, extended pausing is also observed at signaled transitions from a low- to a high-effort response (Wade-Galuska, Perone, & Wirth, 2005).

Despite the generality of this effect, the behavioral processes underlying extended pausing at rich-lean transitions are not well understood. One process that may underlie extended pausing is that the stimuli signaling rich-lean transitions (i.e., the receipt of a large reinforcer followed by a signal correlated with an upcoming small reinforcer) are aversive and temporarily motivate unmeasured escape activities occurring during the extended pause. Because the stimuli accompanying rich-lean transitions signal a relative worsening in reinforcement conditions, Perone (2003) posited that these stimuli are more aversive than stimuli signaling other transitions (e.g., lean-lean). To test this account, Perone added an escape option to the Perone and Courtney (1992) multiple-schedule procedure. Each type of transition was presented 10 times within a session. On half of those occasions, pigeons were given the opportunity to peck an additional key to darken the stimulus signaling the

magnitude of the next programmed food reinforcer, turn the houselight off, and to suspend the reinforcement schedule (an escape response). Another peck on the escape key ended the timeout condition and reinstated the reinforcement schedule. As predicted, escape responses were most frequently observed at signaled rich-lean transitions, providing evidence that the signaled relative worsening in reinforcement conditions is an aversive event. In the no-escape condition, Perone reported extended pausing at signaled rich-lean transitions, with pause durations positively correlated with self-imposed escape durations in the escape condition (r = .72). Thus, in the absence of an explicit escape option, pausing may be a form of escape from the aversive properties of the signaled rich-lean transition.

If extended pausing at signaled rich-lean transitions occurs because the stimuli signaling this transition are aversive, then organisms whose behavior is more sensitive to aversive stimulation should exhibit longer rich-lean pauses. Convergent behavioral and hormonal evidence suggests that Fischer 344 rats' behavior is more sensitive to stressors and aversive stimulation than Lewis rats (for a review see, Kosten & Ambrosio, 2002). Thus, to test the predictive validity of Perone's aversive transition account, we compared rich-lean pauses in Fischer 344 and Lewis rats.

Evidence for a strain difference in response to stressors comes from studies that show Fischer 344 rats defecate more than Lewis rats in stress-inducing novel-open field environments (Rex et al., 1996; Sternberg et al., 1992; Stohr et al., 1998); however, other studies have reported no difference (Chaouloff et al., 1995; Glowa et al. 1992). More consistent strain differences in novel settings are seen with

grooming, where Fischer 344 rats groom more than Lewis rats (Chaouloff, et al., 1995; Glowa et al., 1992; Haile et al., 2001; Sternberg et al., 1992).

Evidence of a strain difference in sensitivity to aversive stimulation comes from an avoidance- and escape-conditioning study. Katzev and Mills (1974) reported that Fischer 344 rats better learned to avoid and escape tone-signaled electric shocks in prompt, delay, and trace conditioning trials by running to a no-shock area of a shuttle box. Fischer 344 rats exhibited shorter avoidance/escape latencies than Lewis rats, but this difference must be interpreted cautiously because Lewis rats were more likely to freeze, rather than run, during the tone. If freezing is the appropriate measure of sensitivity to the aversive tone, then one would conclude that Lewis rats were more sensitive to aversive stimulation.

Other evidence suggesting Fischer 344 rats' behavior may be more sensitive to aversive stimuli comes from a Pavlovian fear-conditioning study. Pryce, Lehmann, and Feldon (1999) compared Fischer 344 and Lewis rats on time spent freezing (i.e., complete motor immobility for 1 s) in four different contexts. On the first day of testing, rats were placed for 30 min in a chamber without shock or programmed stimuli. On day 2, Lewis rats froze more than Fischer 344 rats when a 30-s tone immediately preceded a 1-s foot shock (0.3 mA) followed by a 120-s inter-shock interval during a 27-min session. On day 3, Fischer 344 rats froze longer than Lewis rats in a place conditioning test (8 min in the shock chamber with no shocks or tone) suggesting the Fischer 344 rats better learned the shock-stimulus associations. On day 4, rats were placed in a different no-shock chamber and exposed to the tone

previously paired with the shock for 8 min. Again, Fischer 344 rats froze longer in this test of conditioning to the tone. Further this association was slower to undergo extinction.

Further evidence that shows Fischer 344 rats are more sensitive to aversive stimulation than Lewis rats comes from a study conducted under a Pavlovian conditioned emotional response (CER) paradigm. Stohr et al. (2000) measured suppression of water-maintained licking behavior by a tone previously paired with unavoidable shock. During training (days 1-5), water-deprived rats were given 20 min access to a water bottle. In conditioning (day 6), the water bottle was removed and after 5 and 10 min had elapsed, rats received two light-shock pairings (CS = 10-s flashing light and US = 1-s 0.75-mA shock), in which shock immediately followed the termination of the light. On day 7, rats were given 20 min access to water without the CS or US present. To test for CERs (day 8), rats were placed into the chamber with the water bottle and after 175 licks, the CS was presented for 15 min. The times to complete 25 licks before the CS (Time A: licks 151-175) and 25 licks after the CS (Time B: licks 176-200) were recorded to calculate a suppression ratio [Time A/ (Time A + Time B)] which ranges from 0.5 (no suppression) to 0 (complete suppression), i.e., a stronger CER. Fischer 344 rats exhibited a significantly a greater CER compared to Lewis rats (i.e., 0.07 and 0.22, respectively). In summary, these behavioral results show that Fischer 344 rats' behavior is more sensitive to aversive stimulation than the Lewis rats.

Hormonal evidence also supports that the Fischer 344 rats are more responsive to stressors than Lewis rats. Past studies have indicated a role of the hypothalamic–pituitary–adrenal (HPA) axis in emotional behaviors (Hernan & Cullinan, 1998; for a review see, Kosten & Ambrosio, 2002), a dimension in which the Fischer 344 and Lewis rats are known to differ. Researchers have demonstrated that the HPA axis is activated by stressors: foot-shock, cold water, restraint, predator threat, or novel stimuli (Dunn & Berridge, 1990; Rivier & Plotsky, 1986). Upon activation, the HPA axis releases a hypothalamic corticotropin-releasing factor (CRF) from the paraventricular nucleus (PVN), which stimulates a pituitary adrenocorticotropin releasing hormone (ACTH), which causes the secretion of cortiocosterone (a stress-activated, adrenal glucocorticoid) into the circulatory system. The release of corticosterone helps mobilize the body to resist infection and reduce reactivity to pain. Corticosterone can also prepare an organism to respond to an acute stressor or aversive stimulation. For example, Stone, Egawa, and McEwen (1988) demonstrated that corticosterone injections dose-dependently increased the frequency of escape behavior in rats when their tails were held on a flat surface. Other evidence suggests that repeated exposure to corticosterone may lead to the development of depressive- and anxiety-like behaviors in both humans and nonhuman animals (e.g., Checkley, 1996; Parker, Schatzberg, & Lyons, 2003). Of present interest is research that has shown that Fischer 344 rats release larger levels of corticosterone in response to stressors such as restraint (Stohr et al., 2000) or a novel, illuminated, open-field environment (Chaouloff et al., 1995; Glowa, et al., 1992;

Sternberg et al., 1992) compared to Lewis rats. These hormonal data argue that Fischer 344 rats are more sensitive to stressors and aversive stimulation than Lewis rats.

A potential problem associated with using Fischer 344 and Lewis rats to study Perone's (2003) aversive transition account is a motoric strain difference (e.g., Madden et al., 2008). Such a difference poses a problem for comparing pausing at signaled rich-lean transitions. If the Fischer 344 strain is less active than the Lewis strain, then it would be difficult to interpret longer pauses in the former than the latter strain as due to differences in sensitivity to the aversive characteristics of the rich-lean transitions. Kosten and Ambrosio's (2002) review of the literature on motoric strain differences is mixed. Some studies suggest Fischer 344 rats are less active than Lewis rats (Ambrosio et al., 1995; Camp et al., 1994; Paulus et al., 1998; Rex et al., 1996), but some studies have reported either the opposite (Chaouloff et al., 1995; Haile et al., 2001), or no differences (Kosten et al., 1994; Simar et al., 1996; Stohr et al., 1998). Kosten and Ambrosio warned that these results should be interpreted with caution for two reasons. First, numerous procedural differences existed across studies (e.g., apparatus shape, illumination levels, and time of day). Second, motoric behavior may have been influenced by stress-inducing environments such as a brightly illuminated novel environment (e.g., Rex et al., 1996).

Beyond Kosten and Ambrosio's (2002) review, the current author compared results of studies using similar procedures (e.g., only ones conducted in a novel open-field environment) and found the results are still mixed. Thus, a review of the

literature did not provide conclusive evidence that Fischer 344 rats are less active than Lewis rats. As a result, pausing at rich-lean transitions in these two strains should be attributed to the aversive characteristics of the transitions (i.e., relative worsening in reinforcement conditions).

Given the aforementioned convergent behavioral and hormonal results, Perone's (2003) aversive-transition account predicts that the Fischer 344 rats' behavior should be more sensitive to the aversive stimuli signaling the rich-lean transition and should, therefore, exhibit longer pauses than Lewis rats. To test this prediction, pausing was assessed in Fischer 344 and Lewis rats at four different signaled transitions (rich-lean, rich-rich, lean-rich, and lean-lean) across a range of work requirements (FR 1, 25, 50, 75, and 100) using Perone and Courtney's (1992) multiple schedule procedure.

<center>Method</center>

Subjects

Eighteen male rats (9 Lewis and 9 Fischer 344; Harlan Sprague-Dawley, Indianapolis, IN) were individually housed in plastic cages within a temperature-controlled colony room with a 12:12 hr light/dark cycle. Rats were approximately 18 months old at the start of the experiment and had prior experience choosing between small-immediate and large-delayed food rewards (see Madden et al., 2008). Rats were weighed daily and maintained at approximately 85% of their free-feeding weights by post-session feeding. Water was continuously available between sessions.

Apparatus

Twelve identical operant chambers (Med Associates, St. Albans, VT) were used. Each chamber was 24.1 cm wide, 30.5 cm long, and 21 cm high. One wall was an intelligence panel equipped with a nonretractable center lever (11 cm above the floor) and two retractable side levers (horizontally aligned 11 cm apart and 6.5 cm above the floor). Above each lever was a white, 2-W light (2.5 cm in diameter and 6 cm above each lever). A feeder (Coulbourn, Allentown, PA) delivered 45-mg grain-based food pellets (Bioserve, Frenchtown, NJ) into a receptacle (3 cm wide and 4 cm long) equipped with a 2-W light in the center of the intelligence panel (1 cm above the floor and 10 cm below the center lever). Each chamber was enclosed within a light- and sound-attenuation cubicle (Med Associates) equipped with a ventilation fan and a white noise speaker. A Med Associates® interface system controlled the sessions and collected data.

Procedure

Each session began with a cue light constantly illuminated above the center lever. A center-lever press extinguished the light and initiated the next schedule component (either rich or lean) as one of the side levers was inserted into the chamber. This center-lever response was programmed because some studies have suggested that Fischer 344 rats are less active than Lewis rats (e.g., Rex et al., 1996). To reduce the probability that variability in pausing might be due to motoric differences, the center-lever response ensured that rats were done eating and were active at the moment the multiple schedule-correlated stimuli were presented, were in

a position to observe these stimuli, and were positioned approximately equidistant from levers above which the stimuli were presented.

Center-lever responses were followed by the insertion of either the left or right side lever and the illumination of the cue light above the inserted lever. During a rich schedule-component, the right lever was inserted, the right cue light was continuously lit, and completing the FR requirement resulted in the delivery of 7 pellets over a period of 5.5 s. Upon the initiation of a lean-schedule component, the left lever was inserted, the left cue light flashed (0.25 s intervals), and one food pellet was delivered upon completion of the schedule requirement. After the last pellet was delivered, the center cue light was re-illuminated and the next schedule component could be initiated by pressing the center lever. Across conditions, the FR-schedule values ranged from 1 to 100 and rats were exposed to these conditions according to one of the two sequences shown in Table 1. Within each strain, the assignment of reinforcer magnitude to side levers was counterbalanced.

Table 1.

Sequences of conditions (shown in order of exposure) and the number of

sessions conducted at each condition for each Fischer 344 and Lewis rat.

			Number of Sessions				
Strain	Rat	Seq 1:	FR 50	FR 75	FR 100	FR 25	FR 1
F344	Bl3		27	41	50	-	-
	Bl4		19	23	14	13	-
	Br3		10	14	50	31	16
	Br4		43	41	43	20	17
	Pu2		28	34	24	12	22
Lewis	B3R1		14	18	50	20	15
	Gr2		10	17	10	12	10
	Gr3		21	49	33	13	10
	R1B1		11	10	21	39	16
	R3B1		11	32	50	19	10
Strain	Rat	Seq 2:	FR 50	FR 25	FR 75	FR 100	FR 1
F344	Bl2		33	11	40	50	10
	Br1		44	11	16	50	11
	Pu1		25	42	26	50	14
	Pu3		35	23	50	50	-
Lewis	Gr1		43	10	10	41	10
	Gr4		13	10	34	36	10
	R1B2		19	10	16	18	10
	R2B2		17	10	43	21	10

Pauses were timed from the first center lever press until the first response on the inserted side lever. A session was considered complete when subjects finished all 41 multiple-schedule components in 120 min. or less. Incomplete sessions occurred when subjects failed to complete all the components during a 120 min. session. The sequence of multiple-schedule components arranged within a session was randomly drawn from a pool of 40 different sequences. Each sequence contained either 21 rich- and 20 lean-schedule components (sessions beginning with a rich schedule component), or 20 rich- and 21 lean- components. Each sequence contained 10 of the four possible transitions between multiple-schedule components. That is, 10 times in each session a rich component (7 pellets) was programmed following a rich component (a rich-to-rich transition). Likewise there were 10 rich-lean, 10 lean-lean, and 10 lean-rich transitions. The same type of transition never occurred more than three times in a row. Three Fischer 344 rats (Blue 3, Blue 4, and Purple 3) became ill and their data from unfinished conditions were excluded from data analysis.

Stability criteria. Conditions lasted for a minimum of 10 sessions and until either (a) the median pauses for each of the four types of transitions met both a quantitative and qualitative stability criterion, or (b) after a maximum of 50 sessions. Pauses were considered stable when the average of the final three sessions' median pauses deviated by 5% or less from the preceding three-session average with no trend observed across the last six sessions.

In instances in which incomplete sessions were a frequent event, the criteria were applied to pauses collected across multiple sessions using either (c) the 60 most

recent transitions of each type after a maximum of 50 sessions, or (d) when pauses from the 60 most recent transitions met the aforementioned quantitative and qualitative stability criteria. To assess stability across sessions, pauses were sorted into 6 groups of 10. These groups of 10 pauses were treated as equivalent to the pauses from 6 complete sessions—only Brown 4 met the quantitative and qualitative stability criteria (see criteria d) under these circumstances.

Statistical analysis. Nonparametric Mann-Whitney U tests were used to examine the differences between strains in terms of pausing, center-lever latencies, and running response rates (Howell, 1992). The Mann-Whitney U statistic is defined as the number of pairs (X_i, Y_j) in which $X_i < Y_j$, where X_i and Y_j represent individual rats scores from the Fischer 344 and Lewis strains, respectively.

Results

The numbers of sessions completed at each FR value are shown for individual rats in Table 1. Figure 1 shows median side-lever pauses in the FR 1 condition (error bars correspond to interquartile ranges). The pauses shown in Figure 1, and all subsequent figures, are means of the medians taken from the last six (stable) sessions at each ratio value or from the last 60 completed transitions. The pauses shown in Figure 1 were collapsed across the four transition types to determine if one strain was slower than another in moving from the center- to the side-lever. No significant difference in FR 1 pausing was detected ($U = 564$, $p = 0.34$). Thus, any strain differences observed at signaled rich-lean transitions may more reasonably be

attributed to differences in sensitivity to aversive stimulation rather than to motoric

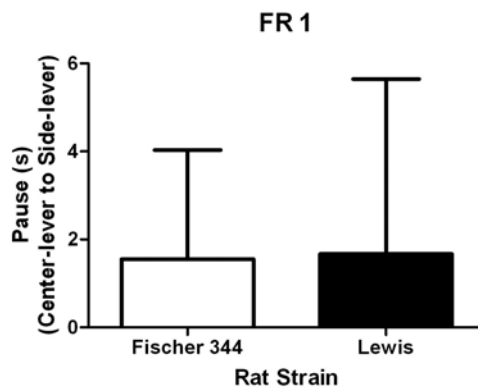differences between the strains.

FR 1

Figure 1. Group median pauses (s) timed from a single center-lever response

to the first response on the inserted side-lever for each strain. Error bars

represent interquartile ranges.

The quadrants of Figure 2 correspond to median pause durations at the four

transitions across the range of FR values explored. Dashed and solid lines connect

median pause durations of the Fischer 344 and Lewis strains, respectively. Upon

visual inspection, both strains paused longer at the rich-lean transition than at the

other transitions at the FR 25, 50, 75, and 100 conditions. Fischer 344 rats paused

significantly longer at FR 25 ($U = 16$, $p = 0.03$), 75 ($U = 26$, $p = 0.02$), and 100 ($U = -15$, $p = 0.02$); however, no difference was found at the FR 50 condition ($U = 26$, $p = 0.22$). At FR 1, Lewis rats paused significantly longer than Fischer 344 rats ($U = 14$, $p = 0.02$). Differences between the strains at the lean-lean control transition tended to

follow the same pattern as the rich-lean transition, with the exception that no

difference was found at FR 25 ($U = 35$, $p = 0.63$). Specifically at lean-lean transitions, Lewis rats paused longer at the FR 1 ($U= 18$, $p = 0.05$), whereas, Fischer 344 rats paused longer at FR 75 and 100 ($U = 13$, $p = 0.02$ and $U = 17$, $p = 0.04$, respectively); again, no difference was found at FR 50 ($U = 33$, $p = 0.51$). At lean-rich transitions, Fischer 344 rats paused longer at FR 50, 75, and 100 than Lewis rats ($U = 9$, $p = 0.01$; $U = 18$, $p = 0.05$; and $U = 10$, $p = 0.01$, respectively). However, no strain differences were obtained at rich-rich transitions (the control transition for lean-rich pauses). Figures 3 (Fischer 344 rats) and 4 (Lewis rats) illustrate the orderly increase in pausing at signaled rich-lean transitions as the FR value was increased at the individual subject level.
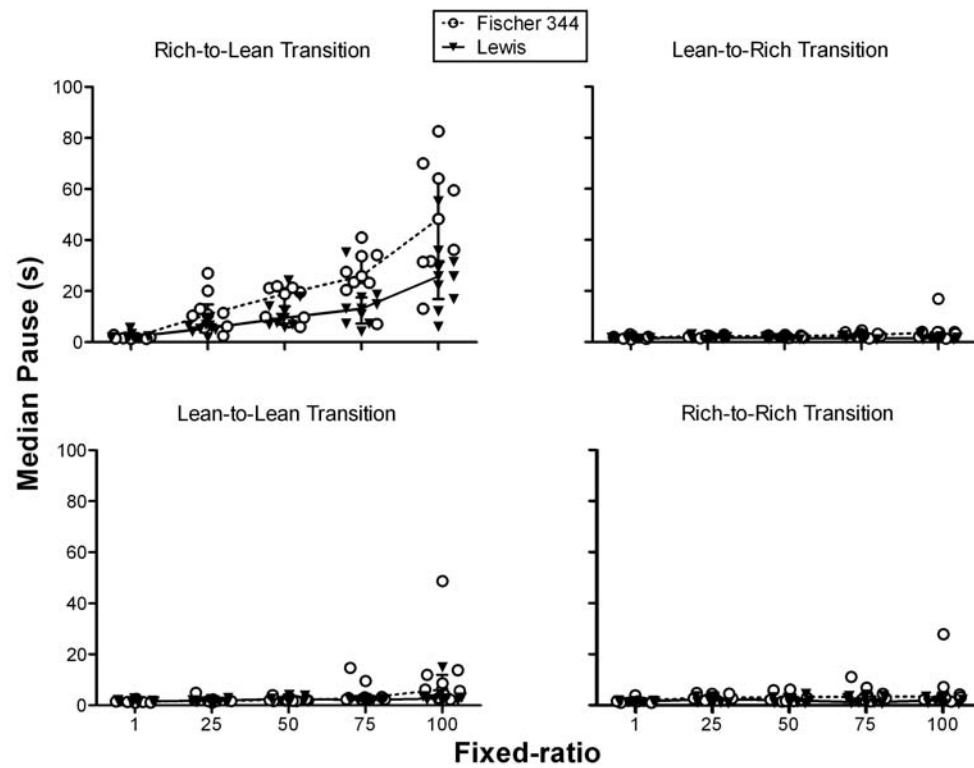
Figure 2. Median pause (s) durations at the four different types of transitions (upper left: rich-lean; upper right: lean-rich; bottom left: lean-lean; bottom right: rich-rich) plotted as a function of FR value. Group median pause durations are connected by dashed (Fischer 344) and solid lines (Lewis). Individual Fischer 344 rats are depicted as open circles (○) and Lewis rats as filled triangles (▼).
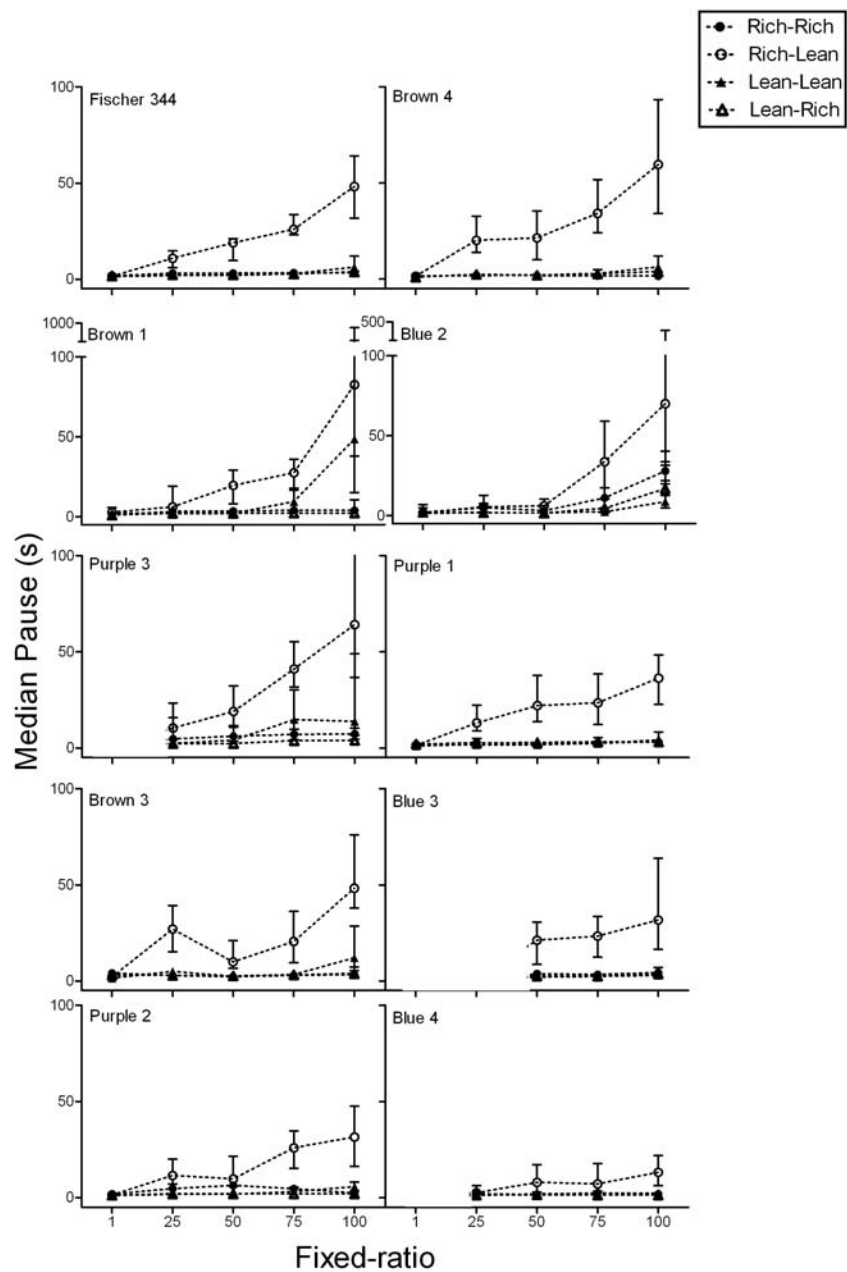
Figure 3. Fischer 344 rats' individual median pause (s) durations across each transition type, plotted as a function of FR value. The group function is shown in the top upper left panel. Note that the y-axis range differs for Brown 1 and Blue 2.
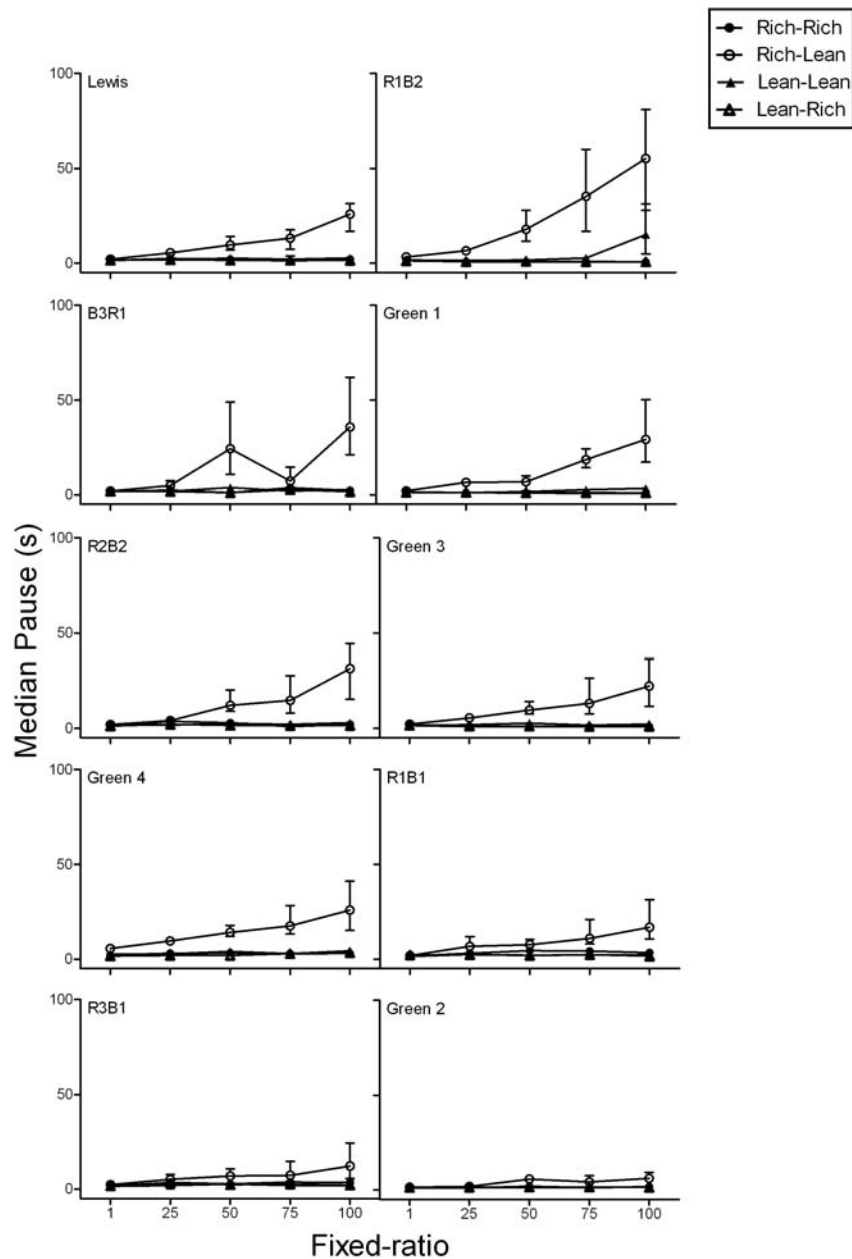
Figure 4. Lewis rats' individual median pause (s) durations across each transition type plotted, as a function of FR value. The group function is shown in the top upper-left panel.

Because pausing obtained at the lean-lean control transition tended to co-vary with pausing at rich-lean transitions at larger FR values (e.g., 75 and 100), the longer pauses emitted by Fischer 344 than Lewis rats should be interpreted with caution. That is, one could argue that long pauses for Fischer 344 rats are simply due to a greater sensitivity to the work requirement when the upcoming reinforcer is lean regardless of whether or not the lean component was preceded by the rich. To address this, individual rats' lean-lean pauses were subtracted from their rich-lean pauses. As shown in Figure 5, Fischer 344 rats still paused significantly longer at the FR 25 ($U = 16$, $p = 0.03$), 75 ($U = 17$, $p = 0.38$), and 100 ($U = 17$, $p = 0.04$) conditions; however, the strain difference at FR 1 value was lost ($U = 26$, $p = 0.20$). Thus, Fischer 344 rats' longer pauses compared to Lewis rats at rich-lean transitions are not due to an increased sensitivity to the work requirement when the upcoming reinforcer was lean.
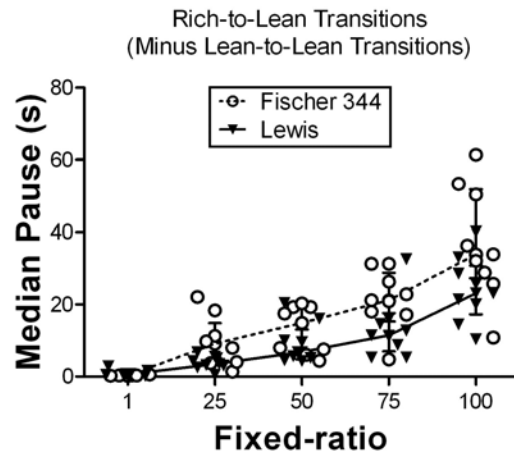
Figure 5. Individual rats' median pause (s) durations at signaled rich-lean transitions plotted as a function of FR value, after pauses at lean-lean transitions were subtracted. Group median pause durations are connected by dashed (Fischer 344) and solid lines (Lewis). Fischer 344 rats are depicted as open circles (○) and Lewis rats as filled triangles (▼).

For individual Fischer 344 and Lewis rats, Figure 6 shows the median latencies to emit a center-lever response following a rich (left panel) or lean reinforcer (right panel). Visually, both strains paused longer after a rich reinforcer than following a lean one (indicative of the longer consumatory interval). Fischer 344 rats had longer center-lever latencies than Lewis rats after both rich (FR 1: $U = 5$, $p = 0.001$; FR 25: $U = 16$, $p = 0.03$; FR 50: $U = 4$, $p = 0.001$; FR 75: $U = 0$, $p = 0.001$; FR 100: $U = 1$, $p = 0.001$) and lean reinforcers (FR 1: $U = 0$, $p = 0.001$; FR 25: $U = 3$, $p = 0.001$; FR 50: $U = 0$, $p = 0.001$; FR 75: $U = 0$, $p = 0.001$; FR 100: $U = 0$, $p = 0.001$).

Because these center-lever latencies across the FR values showed an unexpected U-shaped function, the data were re-analyzed to determine if latencies were a function of the chronological order of exposure to each condition; these data are shown in Figure 7. Visually, center-lever latencies of both strains following a rich reinforcer show a gradual increase across all conditions regardless of the order of conditions. The latencies were especially long in the last two conditions which were FR 25 and FR1 for one group and FR 100 and FR 1 for the other, certainly latency on the FR 1 condition was not a function of the preceding ratio value, rather the length of these latencies was a function of their chronological order of exposure in the experiment.
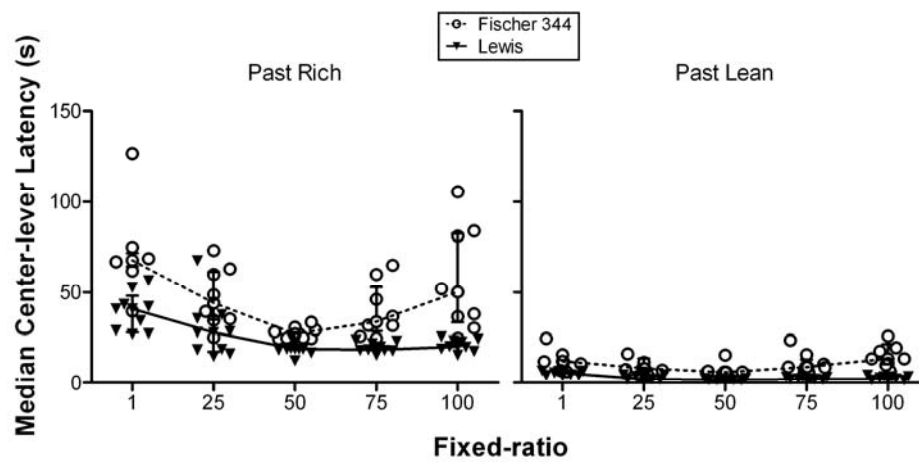
Figure 6. Individual median center-lever latencies (s) following the delivery of either a rich (right panel) or lean reinforcer (left panel) as a function of FR value. Group center-lever latencies (s) are connected by dashed (Fischer 344) and solid lines (Lewis). In both panels, Fischer 344 rats are depicted as open circles (○) and Lewis rats as filled triangles (▼).
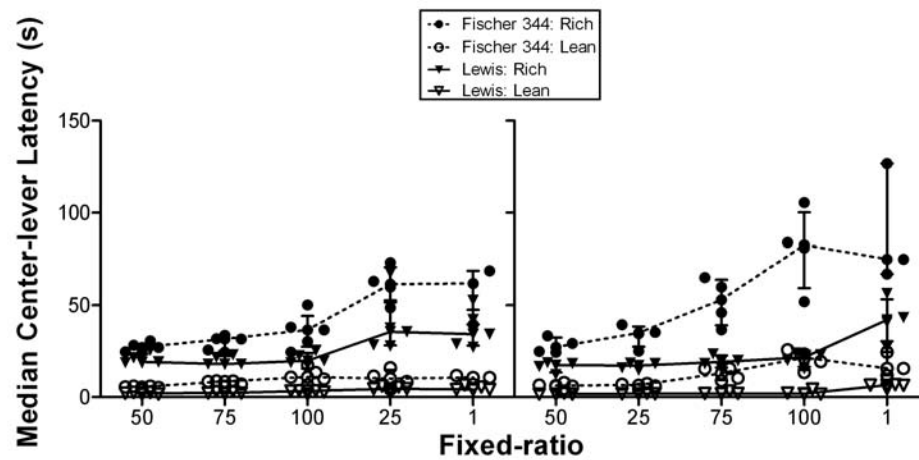
Figure 7. Individual median center-lever latencies (s) following the delivery of either a rich (right panel) or lean reinforcer (left panel) plotted in the sequential order of exposure to each FR value. Group center-lever latencies (s) are connected by dashed (Fischer 344) and solid lines (Lewis). In both panels, Fischer 344 rats are depicted as open (○-past lean) or closed circles (●-past rich) and Lewis rats as open (▽-past lean) or filled triangles (▼-past rich).

Because the center-lever latency data appear to be controlled by the chronological order of exposure to each condition in the experiment, data from signaled rich-lean transitions were re-analyzed to determine if pausing was controlled by the same variables, rather than the FR value. Figure 8 shows that for both strains pauses at signaled rich-lean transitions were controlled by the size of the FR value (i.e., longer pauses were observed as the FR value increased and shorter pause occurred when the FR value decreased). Thus, pausing at signaled rich-lean

transitions for both strains was a function of the FR value and not the chronological

order of exposure to each condition.

To explore the possibility of differences in pausing based on the

counterbalancing of groups, Figure 9 displays the between-strain differences in rich-

lean pausing, separated by the sequence of conditions experienced by each rat (see

Table 1). As before, visually, Fischer 344 rats paused longer at FR 25, 75, and 100

than Lewis rats regardless of the sequence. Within each strain, pauses were

comparable across sequences. The two exceptions were Fischer 344 rats at the FR

100 condition ($U = 2$, $p = 0.05$) and Lewis at the FR 75 condition ($U = 0$, $p = 0.01$)

where pausing was more modest in the sequence described in Figure 9 as "high".
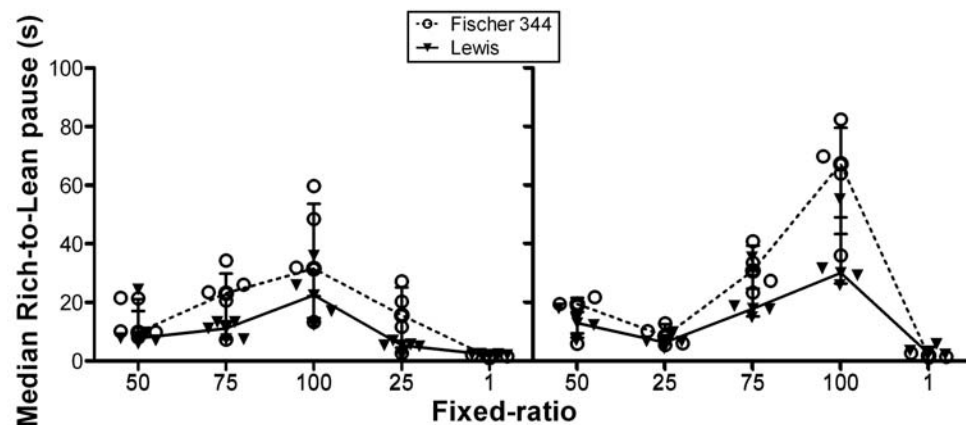

Figure 8. Median pause (s) durations of individual rats at signaled rich-lean

transitions plotted in the sequential order of exposure to each FR value. Group

median pause durations are connected by dashed (Fischer 344) and solid lines

(Lewis). Fischer 344 rats are depicted as open circles (○) and Lewis rats as
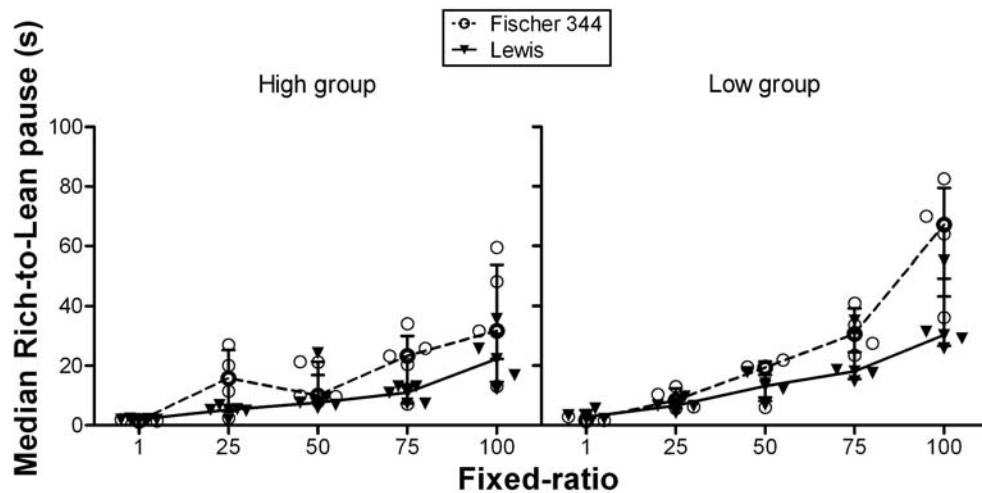
filled triangles (▼).

Figure 9. Median pause (s) durations of individual rats at signaled rich-lean

transitions plotted as a function of FR value. Groups of rats were exposed to

one of two sequences of FR values: FR 50, 75, 100, 25, and 1 (left panel: high

group) or FR 50, 25, 75, 100, and 1 (right panel: low group). Group median

pause durations are connected by dashed (Fischer 344) and solid lines

(Lewis). In both panels, Fischer 344 rats are depicted as open circles (○) and

Lewis rats as filled triangles (▼).

The four panels of Figure 10 display individual Fischer 344 and Lewis rats'

running response rates (response rate excluding pause time) across the four different

transitions at each FR value. Running response rates are taken from the last six

(stable) sessions in each condition or from the last 60 completed transitions. Based on

visual inspection, run rates were undifferentiated across the four different transitions

and did not decrease as a function of the FR value for both strains. Therefore, the data

were collapsed across transition type and FR value. Lewis rats' run rates were significantly higher than Fischer 344 rats ($U = 5179$, p = 0.001).
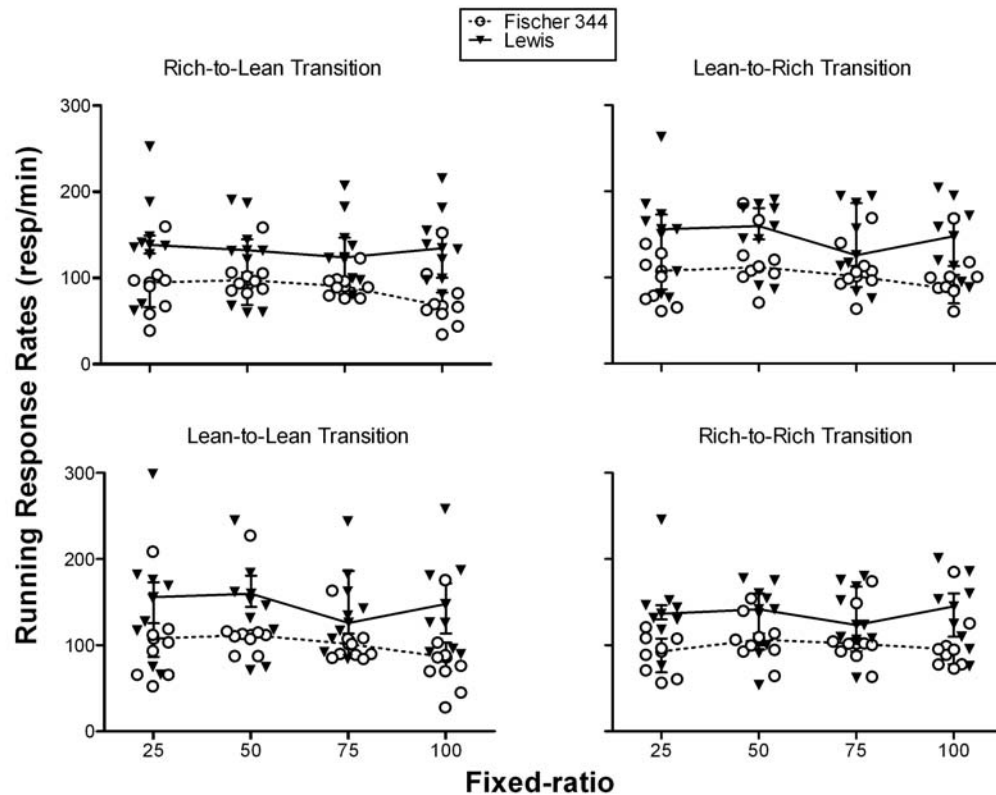

Figure 10. Individual running response rates (resp/min) at the four different types of transitions plotted as a function of FR value. Group running response rates are connected by dashed (Fischer 344) and solid lines (Lewis). In all panels, Fischer 344 rats are depicted as open circles (○) and Lewis rats as filled triangles (▼).

To further characterize the difference in run rates, inter-response time (IRT) distributions (the time between two responses) were calculated across the four different transitions at each FR value and are shown in Figure 11. The group

functions are derived from individual rats' IRTs from the last six (stable) sessions in

each condition or from the last 60 completed transitions. Visually, the shape of the

IRT distribution for both strains was unaffected by either the type of transition or FR

value. When IRTs were sorted into 0.1 s bin sizes, Lewis rats' had significantly fewer

IRT's in the shortest two bins: 0 to 1 s ($U = 0$, $p = 0.001$) and .1 to .2 s ($U = 52$, $p =$

0.01) than Fischer 344 rats. Alternatively, Fischer 344 rats had significantly more

IRTs in the longest bins (3 s or longer: $U = 8$, $p = 0.001$). Thus, slower running

response rates in Fischer 344 rats (compared to Lewis rats) may be accounted by the

more frequent occurrence of relatively lengthy IRTs (3 s or greater) and the less

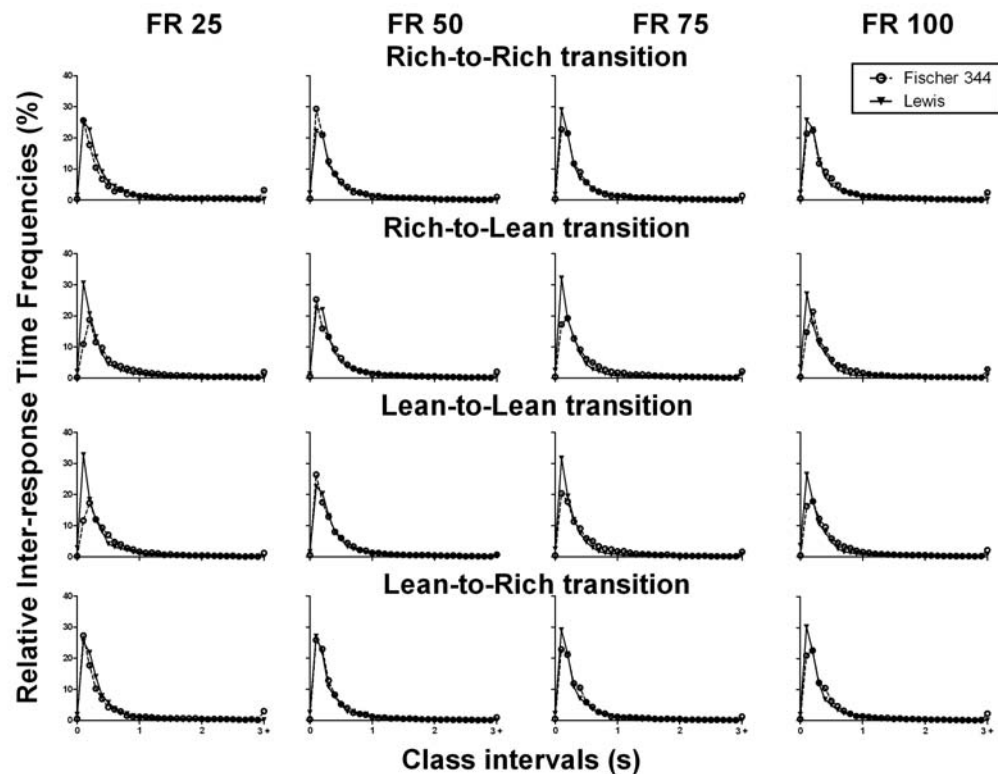frequent short ones (less than 0.1 s).

Figure 11. Relative frequency of IRTs, sorted into 0.1 s bins. The data are organized according to transition type and FR value (left to right: 25, 50, 75, and 100). Group IRTs are connected by dashed (Fischer 344) and solid lines (Lewis). In all panels, Fischer 344 rats are depicted as open circles (○) and Lewis rats as filled triangles (▼).

Discussion

The present study assessed pausing at four different transitions (rich-rich, rich-lean, lean-lean, and lean-rich) in inbred Fischer 344 and Lewis rats across a range of FR values (1, 25, 50, 75, and 100). In both strains, we systematically reproduced Perone and Courtney's (1992) findings of extended pausing at signaled rich-lean transitions. Of critical interest is the aversive nature of signaled rich-lean

transitions and whether organisms whose behavior is more sensitive to aversive stimulation, the Fischer 344 rats, would pause longer at this transition than a comparison group, the Lewis rats. The aversive-sensitive Fischer 344 rats paused longer at signaled rich-lean transitions compared to the Lewis rats, at a majority of the FR values investigated (e.g., 25, 75, and 100). These data support Perone's (2003) aversive-transition account, which argues the signaled relative worsening in reinforcement conditions is an aversive event and that pausing is a form of escape that occurs when no explicit escape option is available. These results also support research suggesting that Fischer 344 rats' behavior is more sensitive to aversive stimulation than is the behavior of Lewis rats (e.g., Stohr et al., 2000).

The strain difference in pausing at signaled rich-lean transitions is not due to the Fischer 344 rats' pauses being more sensitive to the work requirement. Although Fischer 344 rats paused longer than Lewis rats at lean-lean transitions, when these pauses were subtracted from pauses at rich-lean transitions, the strain difference was still significant. Longer pauses by Fischer 344 than Lewis rats at FR 75 and 100 are consistent with research showing that aversiveness of the post-reinforcement pause period increases with FR value (Azrin, 1961; Dardano, 1973; Thompson, 1964). However, the two strains' behavior was not differentially sensitive to the FR value per se because pausing at lean-rich and rich-rich transitions was not different at comparable FR values. Long pauses at lean-lean transitions compared to lean-rich and rich-rich transitions may have occurred because the same amount of work was required for a smaller amount of reinforcement.

Furthermore, the strain difference in pausing at signaled rich-lean transitions is not due to a motoric difference between strains. Two pieces of evidence suggest that Fischer 344 rat's longer pauses at signaled rich-lean transitions are not due to a motoric difference. First, when pauses were collapsed across all four transitions in the FR 1 condition, no significant difference was found between the strains. Second, Lewis rats paused longer than Fischer 344 rats at rich-lean transitions in the FR 1 condition, which is in disagreement with reports that the Fischer 344 rats are less active than the Lewis (e.g., Madden et al., 2008).

At first blush, some researchers might attribute strain differences in run rates and center-lever latencies to a motoric difference. However, the differences in run rates may be accounted for by the more frequent occurrence of relatively lengthy IRTs (3 s or greater) and the less frequent occurrence of short ones (less than 0.1 s) in Fischer 344 rats compared to Lewis rats. As for differences in center-lever latencies, both strains were considered aged at the time of the start of the current study, thus the gradual increase in latencies may reflect the effects of aging. For example, in a different study, age-related deterioration on motor tasks was observed in Fischer 344 rats beginning at 12 to 15 months (Shukitt-Haleetal, Mouzakis, & Joseph, 1998). Our rat strains were 18 months old at the start of the study. Unfortunately, the effects of aging on Lewis rats' motor performance are unknown and predicting the direction of the strain difference in center-lever latencies based on this information awaits further study. Overall, center-lever latencies, running response rates, and IRTs were not controlled by either the transition type or FR value. Thus, these behaviors are not

under the control of the variables that produce extended pausing at signaled rich-lean transitions. Most importantly, pauses at signaled rich-lean transitions are not attributable to the effects of aging (unlike center-lever latencies) because pauses were a function of the FR value and not the chronological order of exposure to each condition in the study.

An unexpected outcome of the study was that Lewis rats paused longer at signaled rich-lean transitions than the Fischer 344 rats in the FR 1 condition which was not predicted by the aversive transition account. There are at least two accounts that may explain why this occurred. First, this finding bears a similarity to results reported in the negative incentive-contrast literature (for a review see, Flaherty, 1996). Freet et al. (2006) assigned Fischer 344 and Lewis rats to groups receiving daily access to either a high-concentration (rich) or a low-concentration (lean) sucrose solution. After several days, both groups were given the lean solution which was an unsignaled rich-lean transition for the former group of rats. For both strains, the rich-lean transition group consumed significantly less of the lean solution than the lean-lean group. Unsurprisingly, the transition from the rich- to a lean-concentration sucrose solution did not increase consumption latencies because no stimuli signaled the transition; rather, consummatory behaviors were disrupted (lower levels of consumption compared to lean-lean controls). In the rich-lean groups, the Lewis rats' consumed significantly less than Fischer 344 rats. These results are similar to the current study if licks are comparable to single lever presses; a comparison which should be made cautiously as these responses may reflect different behavioral

processes (see Rowan & Flaherty, 1991). Second, the strain difference in pausing at FR 1 was relatively small compared to other FR values. Thus, the small FR value was not as aversive as higher ratio values for Fischer 344 rats.

Future research may provide a more direct assessment of the aversive rich-lean transition account with Fischer 344 and Lewis rats by exposing rats to the Perone and Courtney (1992) multiple schedule procedure with an explicit escape option provided (Perone, 2003). If Fischer 344 rats are more sensitive to aversive rich-lean transitions, they should produce more escape responses and spend more time in self-imposed time out than Lewis rats.

To conclude, our findings are consistent with Perone and Courtney's (1992) finding of extended pausing at signal rich-lean transitions. Most importantly, because past research suggests that Fischer 344 rats' behavior is more sensitive to stressors and aversive stimulation (compared to Lewis rats), the present data provide support for Perone's (2003) aversive rich-lean transition account. Moreover, the current findings are likely to contribute to the literature on extended pausing at signaled rich-lean transitions in at least two other important ways. First, our study systematically assessed pausing at rich-lean transitions across a range of FR requirements. Second, given the similar experimental histories between the strains, we have demonstrated potential genetic differences in pausing at signaled rich-lean transitions.

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