MATERNAL NUTRITION AND FOUR-ALTERNATIVE CHOICE

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Two groups of 10 male rats were trained to nose poke for food pellets at four alternatives that provided differing rates of pellet delivery on aperiodic schedules. After a fixed number of pellets had been delivered, 5, 10 or 20 in different conditions of the experiment, a 10-s blackout occurred, and the locations of the differing rates of pellet delivery were randomized for the next component. Two groups of rats were used: The AD group consisted of 10 rats born to dams that had normal (*ad libitum*) nutrition during pregnancy, whereas the 10 rats in the UN group were from dams exposed to reduced food availability during pregnancy. All pups received normal nutrition after birth. Choice between the nose-poke alternatives quickly adapted when the rates of pellet delivery were changed in both groups, but there were no consistent differences in the speed of adaptation between the two groups. The generalized matching relation failed to describe the allocation of responses among alternatives, but the contingency-discriminability model provided a precise description of performance.

Key words: maternal nutrition, choice, generalized matching, contingency discriminability, nose poke, rats

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Following Belke and Heyman (1994), Davison and Baum (2000, 2003) made extensive use of concurrent-schedule procedures in which reinforcer ratios change unpredictably across components during sessions. This procedure, and the analyses that Davison and Baum developed, have provided a precise method of measuring the speed at which choice adapts to changing frequencies, magnitudes, and delays (Davison & Baum, 2000, 2003) of food deliveries on two alternatives, and hence learning under frequently-changing conditions. Using analyses based on the generalized matching law (Baum, 1974), they showed with pigeons that adaptation to changing conditions only took four to five food deliveries to be almost complete.

These procedures and analyses have subsequently been used to measure differences in adaptation rate of offspring as a function of the level of maternal nutrition of dams. Breier et al. (2005) used Davison and Baum's (2000)

procedure in which food rates changed between two alternatives after every 10 deliveries, and the next randomly selected component commenced after a 10-s blackout. One group of rats was composed of offspring of dams with normal maternal nutrition (AD group), and the other of offspring of dams undernourished during pregnancy (UN group). Breier et al. found that the offspring of undernourished dams showed consistently slower adaptation to changes in food ratios on the alternatives over a range of different overall food rates.

Previous research has linked prenatal malnutrition to functional and structural changes in the hippocampal formation (Bronzino, Austin La France, Morgane, & Galler, 1996; DeBassio, Kemper, Tonkiss, & Galler, 1996). Given that it is well known that spatial learning in several paradigms depends on the hippocampus (Long & Kesner, 1998), the present study used an analog to the Davison and Baum (2000) procedure that required more spatial learning. We arranged the same range of reinforcer ratios as used by Davison and Baum (2000) and by Landon & Davison (2001), but used four, rather than two, alternative responses. The food rates at the four alternatives were in the ratio 27:9:3:1, but the order of rates across the alternatives was randomized in each new component. We

expected to see fast adaptation to the new food-rate locations at the start of each component, but a significantly slower adaptation rate in the UN animals.

Steady-state behavior allocation (choice) between two alternatives has been the subject of much research (see review by Davison & McCarthy, 1988), and choice usually is well described quantitatively by the generalized matching law (Baum, 1974). This relation is written as:

$$\frac{B1}{B2} = c\left(\frac{R1}{R2}\right)^{a}, \qquad (1)$$

where B refers to responses, R to reinforcers obtained, with c being a measure of inherent bias and a being a measure of sensitivity to reinforcement (Lobb & Davison, 1975). The value of a usually falls in the range 0.8 to 1.0, and c is usually close to 1.0 (no bias). The same relation has been shown to apply to pairwise behavior allocation in three-alternative choice (Davison & Hunter, 1976), and this result is consonant with Luce's (1959) Principle of Indifference from Irrelevant Alternatives (the constant-ratio rule). This principle states that the choice between two alternatives is unaffected by the provision, or rate, of other alternatives. Pliskoff and Brown (1976) also reported generalized matching on three alternatives with pigeons (reanalysis by Davison & McCarthy, 1988, Table 7.5), but did not assess the constant-ratio rule. Sensitivity averaged 0.85. Finally, H. Miller and Loveland (1974) reported behavior allocation in a single condition using five alternatives with pigeons (reanalysis by Davison & McCarthy, 1988, Table 7.4) and found at least an approximation to generalized matching, with sensitivity values averaging 0.81. These reports indicate, therefore, that pairwise generalized matching occurs with more than two alternatives. We expected similar results here and, following Breier et al. (2005), we expected lower sensitivity values for UN rats than for AD rats.

Two groups of 10 rats were bred and then trained on the four-alternative analog to the Davison-Baum (2000) procedure with 10 pellets per component. Because of an unexpected finding in the first condition, three more conditions (including a replication of Condition 1) were arranged.

METHOD

Subjects

There were two groups of 10 male Wistar rats, which were housed in pairs within groups, with free access to water in their home cages. The AD group was designated by rat numbers commencing with 41, and the UN group by rat numbers commencing with 43. The third digit refers to the cage number, and the last digit refers to 1 of the 2 rats housed in each cage, either 0 or 1. All rats were housed in pairs of litter mates, except for Rats 4310 and 4311, which came from different mothers.

Apparatus

The rats worked in 10 standard MED-Associates (Model ENV-NPW-9L) rat enclosures fitted with an array of nine nose-poke apertures on the left wall, 20 mm above the floor. The experimental chambers were 250 mm wide, 267 mm deep, and 330 mm high. The circular nose-poke apertures were 25 by 25 mm, 21 mm deep, and set 2 mm apart. They were internally lit with a 0.7 W yellow light and, for a response to be effective, the rat's nose had to be inserted 11 mm into the aperture. Only four of the apertures (apertures 2, 4, 6, and 8) were used. On the right wall of the chamber was a centrally located pellet receptacle into which 45-mg standard rat pellets (PJPPP purified formula, Research Diets Inc., NJ, USA) could be delivered. A 2.8-W houselight was also mounted in the center of this wall, 20 mm below the ceiling, to provide ambient light. A fan in the cabinet that contained the experimental chamber provided ventilation and masked external noise. All experimental events were arranged, and all data (the time of every experimental event) were collected, by remote PC-compatible computers running MED-PC IV.

Procedure

Sessions were conducted at the same time each day and ended in blackout after 80 pellets had been obtained, or after 1 hr, whichever came sooner. Following sessions, each pair of rats was allowed 2 hr free feeding (standard lab chow) in their home cages, and then were given no further food until the start of the next session.

Nutritional manipulation. Virgin Wistar rats were time-mated at 100 ± 5 days of age, and after confirmation of mating were housed individually in standard rat cages with free access to water. Rats were randomly assigned to groups either that continued to receive standard rat chow (Teklad 18% Protein Diet, Oxon, UK) *ad libitum* (AD group) or that received 30% of the mean intake of the AD group on that day throughout gestation (UN group; Vickers, Breier, McCarthy, & Gluckman, 2003; Woodhall, Breier, Johnston, & Gluckman, 1996). After birth, litter size was adjusted to 8 pups per litter to standardize nutrition until weaning. Pups from UN dams were cross-fostered onto AD dams to provide the same nutrient-rich environment after birth as AD offspring. Ten male AD and 10 male UN offspring were used for this study. The cages were made from hard plastic with metal bar tops and water always available. From weaning until 60 days of age, standard rat chow was provided *ad libitum.* Food access was then restricted to 2 hr after the daily experimental sessions. All rats were exposed to a 12-hr light/ dark cycle with lights on at 0600 and off at 1800. This study was conducted in accordance with guidelines approved by the University of Auckland Animal Ethics Committee.

Reinforcement contingencies. The rats were placed on a limited feeding routine of 2 hr/ day from the age of 61 days onwards, and were magazine trained and autoshaped to nose poke to the four apertures lit yellow. After 10 days' training on continuous reinforcement, the schedule was progressively increased to VI 27 s, and changeover delays (Herrnstein, 1961) between the alternatives were instituted and increased to 2 s. The experiment began at about an age of 105 days.

Within sessions, the overall rate of arranged reinforcers was VI 27 s. Reinforcers arranged on this schedule were allocated, via probability gates, to the four nose-poke apertures in the ratio 27:9:3:1 (probabilities of .675, .225, .075, and .025, respectively). There are 24 ways in which these reinforcer probabilities can be allocated to the four nose-poke apertures, and one of these was arranged (without replacement) for each of the components that comprised a session. In Conditions 1 and 4, there were 10 food pellets per component, in Condition 2 there were 20, and in Condition 3 there were 5. Each component was followed by

a 10-s blackout before the start of the next component. Nose-poke apertures were illuminated and the houselight was lit when responses could produce pellets; all lights were extinguished during blackouts. Training was carried out using this procedure for 45 sessions (Conditions 1 & 2) and 30 sessions (Conditions 3 and 4). Sessions ended after 80 pellets had been delivered (i.e., after eight components in Conditions 1 and 4, after four in Condition 2, and after 16 in Condition 3), or after 60 minutes, whichever occurred sooner. When sessions ended on the time criterion, data from the uncompleted component(s) were not used in analyses.

RESULTS

Data from the last 15 sessions of each condition were analyzed for each rat. For an initial analysis, the numbers of responses emitted to each reinforcer probability, independent of nose-poke location, were summed for each successive reinforcer for each group. That is, all responses on the highest reinforcer-probability alternative for each successive reinforcer were summed, and so on. Because all reinforcer rates were arranged for each of the four nose pokes, this analysis should be independent of any inherent differences in preference between the four nose-poke responses. The probabilities of responding to each of the food probabilities as a function of successive pellets delivered in the components is shown in Figure 1 for all four conditions. Response proportions commenced, before the first pellet was delivered, at about .25 which represents random allocation between the four alternatives. Response proportions changed rapidly within components, and reliable differentiation was obtained after just 1 or 2 pellets. Adaptation was clearly incomplete after the final pellet delivery in the conditions with 5 and 10 pellets per component, and may have been incomplete on the highest reinforcer rate in the 20 pellets per component condition. In the 20-pellets condition, response proportions clearly would not stabilize at values equal to reinforcer proportions (i.e., strict matching) even with more component reinforcers—for example, it seems very unlikely in Condition 3 that the proportional choice of the highest probability of pellets would reach .675, and that choice for the
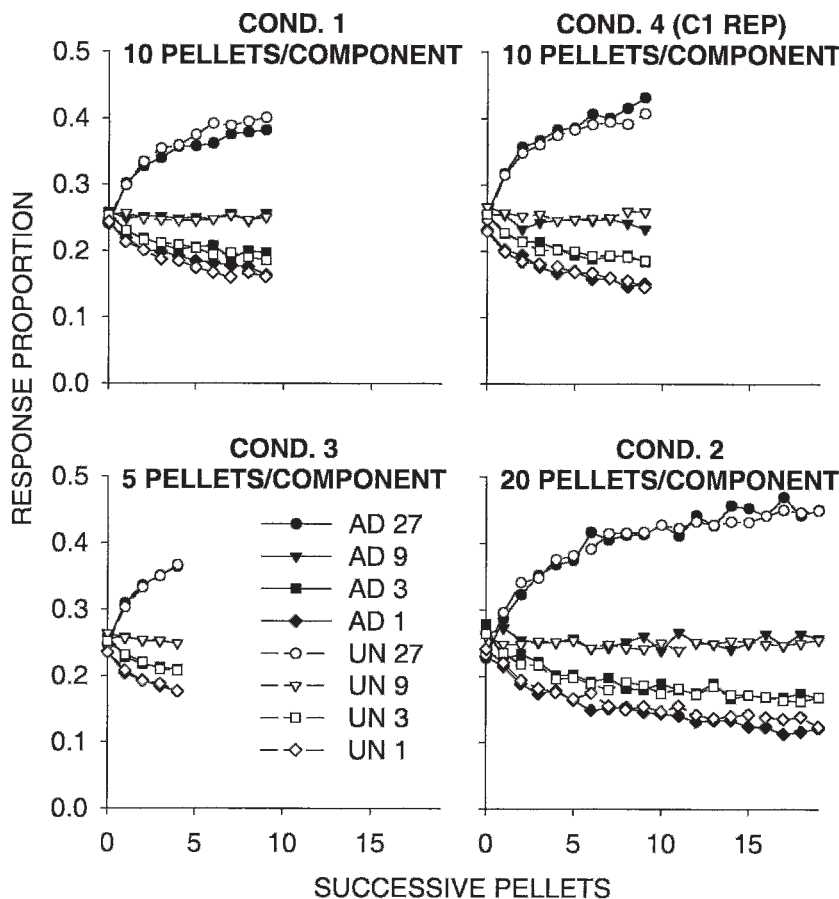
Fig. 1.   Proportions of responses emitted to the four-alternative reinforcer rates as a function of the number of pellets delivered in all four conditions of the experiment, shown separately for the two groups. The data have been averaged over the 10 rats in each group.

lowest probability would reach .025. Response proportions were marginally more extreme in Condition 4 than in Condition 1.

Figure 1 shows that the UN rats showed faster adaptation within components than the AD rats when we arranged 10 pellets per component in Condition 1, but there were no systematic differences in the replication of this condition (Condition 4), nor in Conditions 2 and 3. The difference in Condition 1 was in the opposite direction to that reported for the two-alternative procedure by Breier et al. (2005).

Figure 2 shows selected data from Condition 1 for some individual rats plotted in the same way as Figure 1. We randomly selected rat numbers 10, 21, 40 and 51 for each AD (41), and UN (43) group. All four pairs of rats

showed similar fast adaptation to the differing reinforcer probabilities as the group mean, although the speed of adaptation differed (see particularly Rats 4121 and 4321). Of the data shown in Figure 2, only UN Rats 4310 and 4340 showed faster adaptation to lower probabilities of pellets than their numerical AD counterparts, and Rat 4340 showed a more complete adaptation to the higher pellet probability. However, statistically, using the group mean data (Figure 1), the choice proportions for the UN rats were more extreme (further from .5) than those for the AD rats for all 10 successive reinforcers for the .025 and .075 probability alternatives and for 9 of the 10 successive reinforcers for the $p = .675$ data (Sign Test, all $p < .05$). The same test found no significant differences for any other
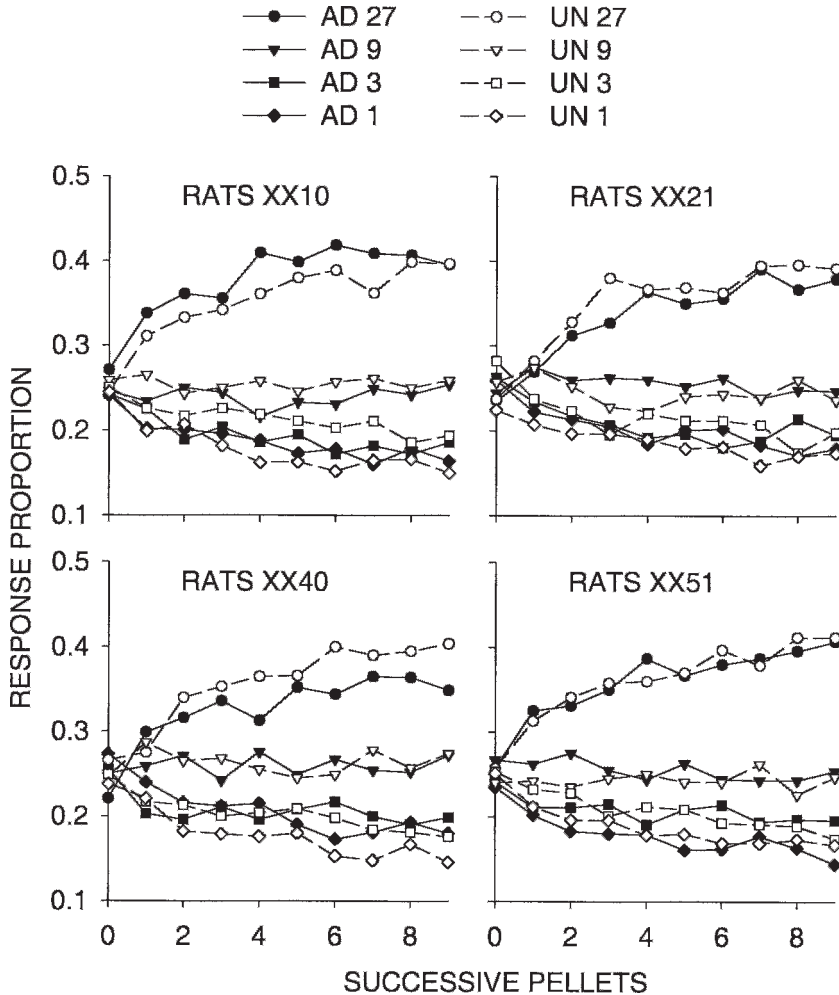
Fig. 2.   Proportions of responses emitted to the four-alternative reinforcer rates as a function of the number of pellets delivered in all four conditions of the experiment, shown separately for the two groups. The data are for 8 individual rats, 4 from each group.

condition. The similarity of results for individuals and groups justifies the subsequent use of group data analyses in this paper.

Previous research suggests that response distributions between all pairs of alternatives as a function of distributions of reinforcers between the alternatives should follow the generalized matching law (see Davison & McCarthy, 1988). Additionally, sensitivity to reinforcement should increase as more pellets are obtained in components (Davison & Baum, 2000). The generalized matching law (Baum, 1974) might be fitted to all pairwise alternatives as a function of reinforcer number, but Schneider and Davison (2005) sug-

gested a more appropriate analysis. Following Natapoff (1970), they proposed that the appropriate generalization of the generalized matching law for n alternatives was:

$$\frac{B_i}{\sqrt[n]{\prod\limits_{n}^{i=1} B_i}} = c \left(\frac{R_i}{\sqrt[n]{\prod\limits_{n}^{i=1} R_i}} \right)^a, \qquad (2)$$

where a is sensitivity to reinforcement and c measures bias. The subscript i denotes the different reinforcer frequencies, rather than response locations, so c should be 1 in the present data because each of the four sched-
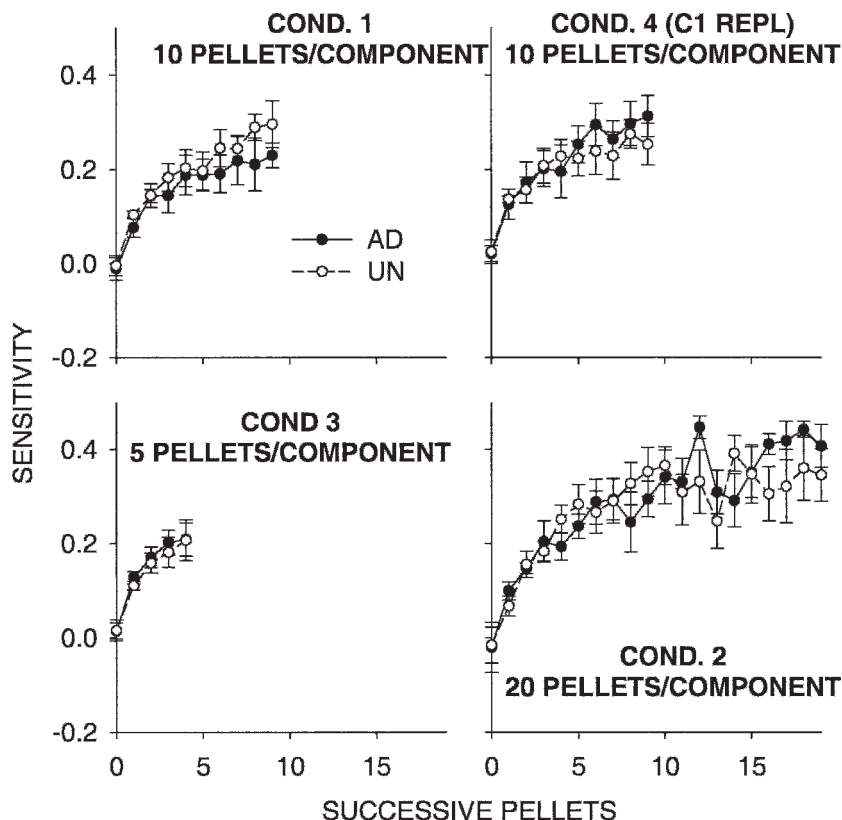
Fig. 3. Sensitivity to reinforcement, and standard errors of these measures, for the group data as a function of successive pellet delivery in components. Sensitivity was measured using Equation 2. Data for the two groups are shown separately.

ules was arranged to occur equally often on each of the four nose-poke apertures. Sensitivity values were estimated by linear regression to the logarithmic transform of Equation 2, assuming $c = 1$. Overall programmed reinforcer-frequency ratios were used as the independent variable. This analysis was conducted for responding between each successive pellet delivery (i.e., sensitivity to pellet 1 was obtained from responses emitted between the delivery of pellets 1 and 2). The results of this analysis are shown in Figure 3. Sensitivity increased with the number of pellets delivered in components as expected from the two-alternative results reported by Davison and Baum (2000), and there were no reliable differences across conditions in the speed at which sensitivity changed with pellet delivery number.

However, analysis using Equation 2 may be inappropriate. Figure 4 shows a further analysis of log response ratios on some pairwise

alternatives as a function of log reinforcer ratios. The data used were choice ratios after the last three pellet deliveries in components—for example, in Condition 1, after pellets 7, 8 and 9. It is evident from Figure 4 that the choice functions in all conditions were very different in shape depending on whether the data were plotted pairwise as the lowest reinforcer frequency versus the other, higher, reinforcer frequencies, or whether they were plotted pairwise as the highest reinforcer frequency versus the others. Note that, because the data could not be affected by bias, the data obtained, for example, from a 9:1 reinforcer ratio, were plotted both as this ratio and as a 1:9 reinforcer ratio by multiplying both log response and log reinforcer ratios by -1. Of course, 27:1 and 1:27 are common to both series of plots. It is clear that a single straight line cannot describe all the data. For instance, a 9:1 reinforcer ratio could come

FINAL 3 INTER-REINFORCER INTERVALS

———●——— AD R27 vs R1, R3, R9
———○——— UN R27 vs R1, R3, R9
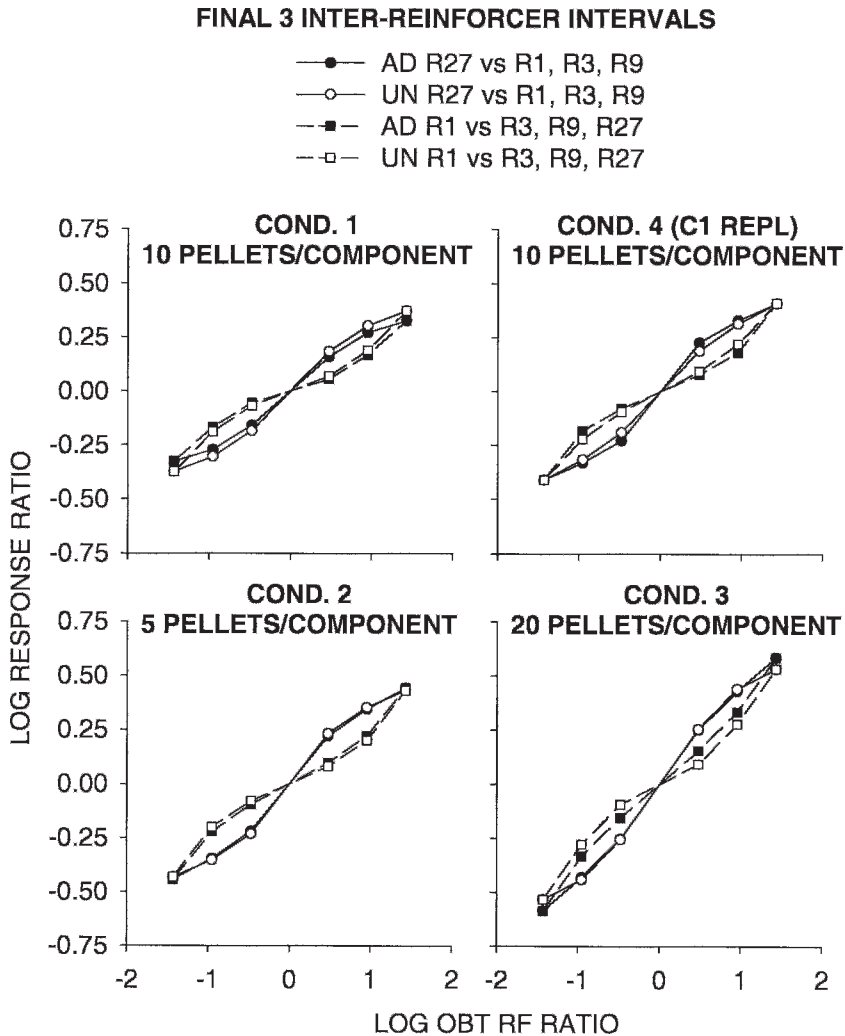— –■ – — AD R1 vs R3, R9, R27
— –□ – — UN R1 vs R3, R9, R27

Fig. 4. Group average log response ratio collapsed over the last three pellet deliveries in components as a function of obtained log reinforcer ratio. Two functions are shown: One used the lowest reinforcer probability versus higher probabilities; the other used the highest reinforcer probability versus lower probabilities. Data from each condition, and for the two groups, are shown separately. Because there could be no response bias in these data, both the data and their inverses are shown. Thus, data for the 9:1 reinforcer ratio also are plotted as a 1:9 ratio, with the log response and reinforcer ratios being multiplied by -1. Data from 9:3 and 3:9 ratios are not shown as they do not belong to either data set.

from a combination of 27:3 or 9:1. The former consistently produced more extreme choice than did the latter for both groups of rats. Because the generalized-matching relation deals only with ratios of reinforcers, it must predict that these two data points will superimpose. However, it did again appear that the performance of the UN rats was more sensitive than that of the AD rats in Condition 1 (log response ratios were more extreme), as noted in relation to Figure 1.

Thus, generalized-matching analysis of these data (Figure 4) is inappropriate because of systematic deviations from the expected single straight line. It could be argued that this might have occurred because we used transition-state, rather than steady-state, data, and that choice had not stabilized by the end of components even when 20 pellets per component were arranged (Condition 3). An argument against this is the finding that generalized matching described transitional data in

the procedure used by Davison and Baum (2000, 2003). It is clear that the rats' task was, in some sense, to discriminate the locations of the differing pellet frequencies at the alternatives and, although they did this remarkably well, the discrimination remained imperfect—sensitivity values at the end of components were noticeably lower than expected in concurrent VI schedules, and they may still have been increasing even after 20 pellets in a component.

Assuming that the rats were adapting to changed response–reinforcer relations during components, a model that attends directly to these relations may be more appropriate. Such a model is the contingency-discriminability model introduced by Davison and Jenkins (1985) and discussed fully by Davison and Nevin (1999). The basic model for two alternatives is:

$$\frac{B_1}{B_2} = c\frac{d_{br}R_1 + R_2}{d_{br}R_2 + R_1}. \qquad (3)$$

The variables in this model are the same as for Equation 2, but d_{br} (which effectively replaces the work done by a) measures the degree to which an animal discriminates the relation between responses emitted and reinforcer frequencies obtained. The value of d_{br} ranges from 1.0 (no response–reinforcer discriminability) to infinity (perfect discriminability). If we assume that the rats are discriminating between stimuli on a unitary dimension of reinforcer frequency, we can assume that d_{br} values between pairs of pellet frequencies combine multiplicatively, for instance $d_{br9,1} = d_{br9,3} \cdot d_{br3,1}$ (Davison & Nevin, 1999). The model, when applied to four alternatives, is too long to reproduce here, but, for example, the ''effective'' reinforcer rate (R'_{27}) for the highest reinforcer-rate alternative is:

$$R'_{27} = R_{27} + \frac{R_9}{d_{br27,9}} + \frac{R_3}{d_{br27,9} \times d_{br9,3}}$$
$$+ \frac{R_1}{d_{br27,9} \times d_{br9,3} \times d_{br3,1}}$$

and response ratios simply equal the ratios of effective reinforcer rates between alternatives (Davison & Nevin, 1999). This model has the potential to describe the present data because, if discriminabilities are less than infinite, a particular obtained reinforcer ratio does predict differing response ratios depending on the context in which this reinforcer ratio
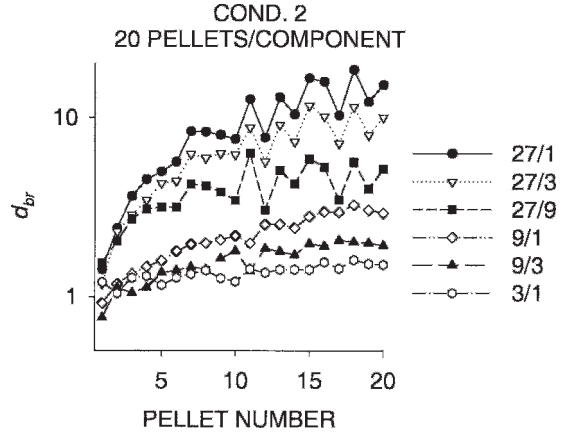

Fig. 5. The value of d_{br}, fitted by nonlinear regression following Equation 3, for the grouped Condition 2 AD data. d_{br} values for 27:9, 9:3 and 3:1 were fitted, and the values for the other pairs of alternatives were calculated from these (see text).

occurs—that is, that 27/3 will produce a different choice from 9/1.

Equation 3 was fitted in logarithmic terms to the data from each condition and between each pellet delivery using nonlinear regression. Three parameter values were estimated: $d_{br27,9}$, $d_{br9,3}$, and $d_{br3,1}$, with other discriminabilities calculated from these as described above (that is, the d_{br} value used for 27:3 was $d_{br27,9} \cdot d_{br9,3}$), for 27:1 it was $d_{br27,9} \cdot d_{br9,1}$), and for 9:1 it was $d_{br9,3} \cdot d_{br3,1}$. Equation 3 fitted excellently, with very high percentages of variance accounted for beyond pellet #2 (there was very little data variance to account for following pellets 0 and 1). Figure 5 and Table 1 show the results of our analysis of the data from Condition 2 (20 pellets/component). Figure 5 shows that group d_{br} values increased from around 1.0 prior to the delivery of any pellet to higher values: The highest discriminability was between the 27 and 1 alternatives, the lowest between the 3 and 1 alternatives, with the others intermediate. As may be expected (Figure 4), d_{br} for the 27:3 alternatives was higher than for the 9:1 alternatives, and the values for the 27:9, 9:3 and 3:1 were ordered respectively. Note that the d_{br} values for 27:3, 27:1, and 9:1 were calculated from the fitted values, and therefore the first two of these reflect the variability of $d_{br27,9}$ across pellet deliveries. Table 1 provides further detailed information on fits to individual-rat data in Condition 2, focusing

Table 1

Data from Condition 2 (20 pellets per component) analyzed according to Equation 3, and the mean of these for each group. Fits to the data averaged across subjects in each group also are shown. The left columns show Equation 3 fits to data collapsed across pellets 7, 8 and 9; the right columns show fits for data collapsed across pellets 17, 18 and 19. Rat numbers commencing 41 belong to the AD group, those commencing 43 to the UN group. VAC is the proportion of data variance accounted for.

Rat #	Pellets 7, 8, 9				Pellets 17, 18, 19			
	$d_{r27,9}$	$d_{r9,3}$	$d_{r3,1}$	VAC	$d_{r27,9}$	$d_{r9,3}$	$d_{r3,1}$	VAC
4110	4.008	1.692	1.317	0.999	8.699	2.667	2.208	0.999
4111	2.858	1.438	1.027	0.998	2.150	1.855	1.307	1.000
4120	5.337	1.546	1.138	1.000	4.566	1.838	1.524	1.000
4121	6.469	1.588	1.349	1.000	17.410	1.874	1.634	0.999
4130	6.889	1.697	1.521	1.000	9.843	1.916	1.372	1.000
4131	2.288	1.926	1.000	0.991	4.425	2.103	1.076	0.975
4140	2.219	1.855	1.413	1.000	3.031	2.802	2.039	0.995
4141	1.938	1.288	1.219	1.000	2.936	2.986	2.135	0.999
4150	8.892	1.413	1.982	1.000	3.148	1.645	2.125	1.000
4151	3.678	1.645	1.301	0.996	27.619	2.025	1.526	0.979
4310	2.858	1.438	1.027	0.998	2.150	1.855	1.307	1.000
4311	5.337	1.546	1.138	1.000	4.566	1.838	1.524	1.000
4320	6.469	1.588	1.349	1.000	17.410	1.874	1.634	0.999
4321	6.889	1.697	1.521	1.000	9.843	1.916	1.372	1.000
4330	2.288	1.926	1.000	0.989	4.425	2.103	1.076	0.975
4331	2.219	1.855	1.413	1.000	3.031	2.802	2.039	0.995
4340	1.938	1.288	1.219	1.000	2.936	2.986	2.135	0.999
4341	8.892	1.413	1.982	1.000	3.148	1.645	2.125	1.000
4350	3.678	1.645	1.301	0.996	45.000	2.625	1.466	0.993
4351	4.767	1.379	1.537	1.000	4.218	2.319	1.371	1.000
AD Mean	4.458	1.609	1.327		7.513	2.116	1.638	
UN Mean	4.533	1.578	1.349		9.673	2.196	1.605	
Group fitted:								
AD	3.595	1.588	1.286	1.000	4.750	2.086	1.577	0.998
UN	4.892	1.639	1.257	1.000	4.339	2.154	1.282	1.000

on data collapsed across pellet deliveries 7, 8, and 9, and 17, 18, and 19. Again, the fits were excellent, and d_{br} values were almost invariably perfectly related to the separation of the pellet-delivery rates.

DISCUSSION

First, the data reported here found no reliable differences as a function of maternal nutrition in the speed of adaptation to changes in the locations of differing reinforcer rates. This was a surprising finding because we previously have reported that the offspring of undernourished rat dams adapted significantly more slowly compared to offspring from fully nourished dams in a two-alternative procedure (Breier et al., 2005). Further research will be needed to follow up this difference.

The distribution of behavior between the alternatives systematically deviated from the generalized matching law (Figure 4). Pairs of same-ratio alternatives with higher overall reinforcer rates (e.g., 27 vs. 9) gave more extreme behavior allocation than did those with lower overall reinforcer rates (e.g., 9 vs. 3). One possibility is that this occurred simply because allocation did not reach asymptote even in 20-pellet components (Condition 2). If this was so, then we would expect to see systematic deviations between same-ratio alternatives decrease across successive pellet deliveries in components. Figure 6 shows log response ratios in Condition 2 before pellets 1, 2, 4, 8, 16, and 20. The pattern of responding changed progressively between pellets 1 to 8: First, the overall functions became steeper, and second, whereas response ratios for the 27:9 and 27:3 reinforcer ratios (open circles) at pellet #1 were above those for the 3:1 and 9:1 reinforcer ratios (filled circles) on the left of the graphs (and vice versa on the right of the graphs), this relation reversed as more pellets were delivered in components. There
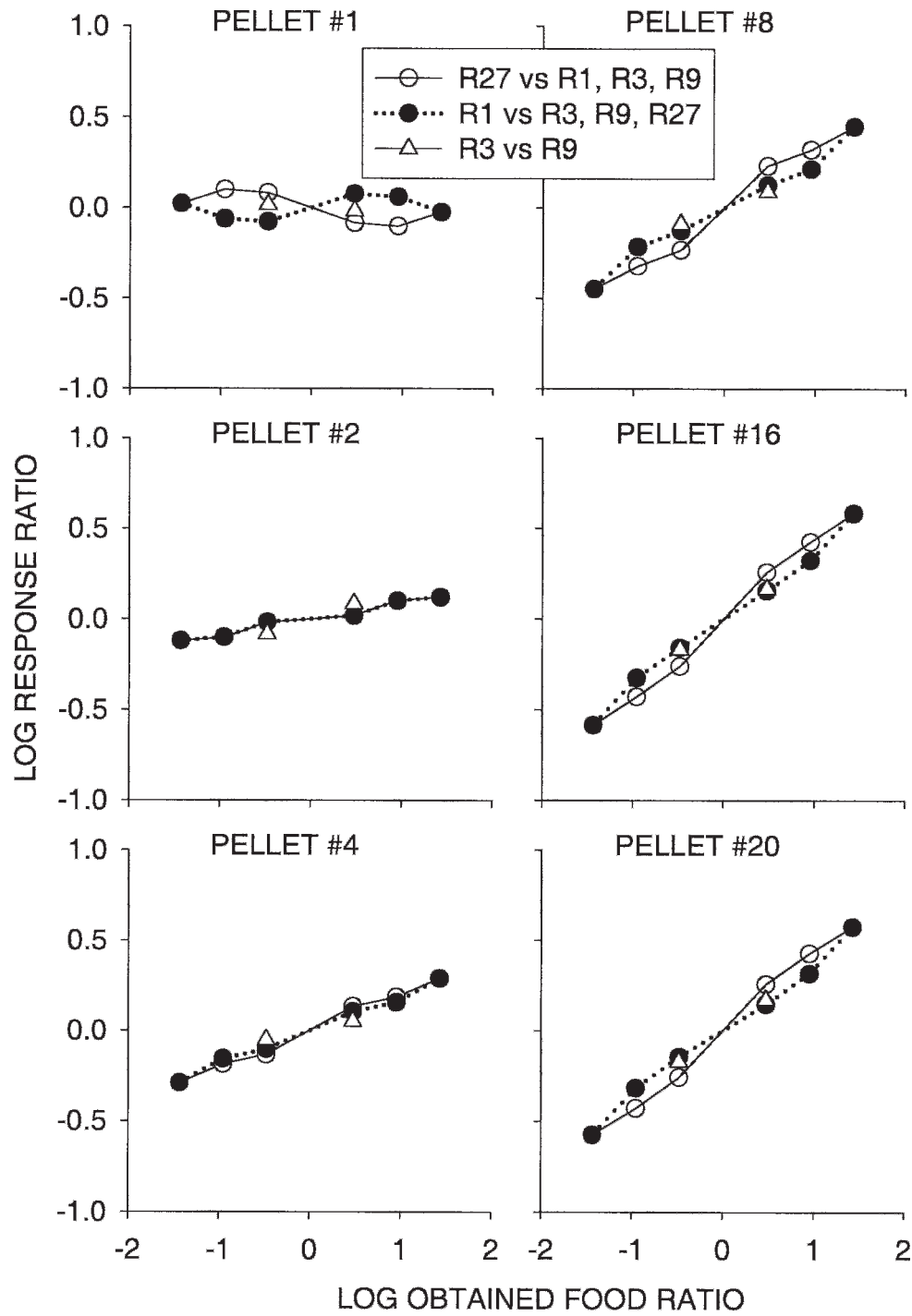
Fig. 6. Log response ratios as a function of overall log reinforcer ratios prior to selected pellet numbers delivered within components. The data used were from the AD group in Condition 2. As in Figure 4, both the data and their inverses are plotted.

was little change beyond pellet 8, and none at all between pellets 16 to 20. It remains possible that the two functions would have moved together if components were much longer than arranged here, and we are currently investigating this possibility in a steady-state concurrent-schedule experiment.

Increasing allocations of behavior (and sensitivity to reinforcement) at higher overall reinforcer rates in two-alternative schedules has been reported previously (Alsop & Elliffe, 1988; Elliffe & Alsop, 1996). This superficially appears to be a similar effect to our finding of greater choice between higher reinforcer-rate pairs. However, an explanation in terms of total reinforcer rate fails for the present data because the overall reinforcer rate over all four alternatives remained constant.

The present results imply that the constant-ratio rule (Luce, 1959) does not generally apply, despite previous research on three alternatives that has supported it (Davison & Hunter, 1976). If reinforcer ratios in the context of lower reinforcer rates produce more sensitive behavior allocation than do the same ratios in the presence of higher reinforcer rates, then the results of Alsop and Elliffe (1988) and Elliffe and Alsop (1996) follow: Extraneous reinforcer rates will be relatively lower when food reinforcer rates are high, and relatively higher when food reinforcer rates are low, producing higher preference (and sensitivity to reinforcement) at higher reinforcer rates.

Why, then, has the constant-ratio rule found support in the study of three-alternative choice (Davison & Hunter, 1976)? The answer may lie in the appropriate model for behavior allocation. The present data were very well described by the contingency-discriminability model (Equation 3; Table 1), but with generally quite low discriminability values (Figure 4; Table 1). These low values are understandable because the discrimination between four differing reinforcer rates, each scheduled on a variable-interval schedule, will necessarily be difficult. In the contingency-discriminability model, the degree to which the constant-ratio rule will be supported depends on the value of contingency discriminability—higher d_{br} values produce less deviation from the constant-ratio rule. In two-alternative concurrent VI VI schedules, d_{br} is usually in the range 10 to 50 (e.g., Davison & Jenkins, 1985). In switching-key concurrent VI

VI schedules, in which each alternative is signalled by a different stimulus, d_{br} depends on the physical difference between the stimuli (Alsop & Davison, 1991; J. Miller, Saunders, & Bourland, 1980), so support for the constant-ratio rule may be more difficult to find. Indeed, in an unpublished dissertation, Murrell (1995) failed to find support for the constant-ratio rule in a series of three-alternative concurrent VI VI VI schedules using switching-key procedures. Finally, theoretical analyses of Equation 3 show that the degree to which the constant ratio rule is violated in two-alternative schedules is small (and will likely fall within error variance) with d_{br} values > 10.

In summary, then, significant violations of the constant-ratio rule—and failure to support generalized matching—will occur whenever response–reinforcer relations are imperfect or poor. Violations like those seen here cannot be seen in two-alternative choice, will be unlikely to be found in three-alternative location choice, will be more likely to be found in three-alternative stimulus choice, and will be likely in >3 alternative choice generally. In the three-alternative case, deviations from the constant-ratio rule cannot be seen in single conditions, and require a series of conditions in order that a sensitivity change can be measured. We propose, therefore, that the general model of choice is the contingency-discriminability model (Davison & Jenkins, 1985) rather than the generalized matching law (Baum, 1974). It could be, as Baum, Schwendiman, and Bell (1999) suggested, that sensitivity values less than 1.0 (a degree of undermatching) will still occur when the discrimination of alternatives is expected to be perfect. However, our analysis implies that such undermatching could arise from higher-than-usual extraneous reinforcer rates even with high contingency discriminability. Finally, it is worth noting that studying four-alternative choice has considerable benefits because effects seen in such complex choice may either be hard, or impossible, to see in simpler choice situations.

REFERENCES

Alsop, B., & Davison, M. (1991). Effects of varying stimulus disparity and the reinforcer ratio in concurrent-schedule and signal-detection procedures. *Journal of the Experimental Analysis of Behavior, 56,* 67–80.

Alsop, B., & Elliffe, D. (1988). Concurrent-schedule performance: Effects of relative and overall reinforcer rate. *Journal of the Experimental Analysis of Behavior, 49,* 21–36.

Baum, W. M. (1974). On two types of deviation from the matching law: Bias and undermatching. *Journal of the Experimental Analysis of Behavior, 22,* 231–242.

Baum, W. M., Schwendiman, J. W., & Bell, K. E. (1999). Choice, contingency discrimination, and foraging theory. *Journal of the Experimental Analysis of Behavior, 71,* 355–373.

Belke, T. W., & Heyman, G. M. (1994). Increasing and signaling background reinforcement: Effect on the foreground response-reinforcer relation. *Journal of the Experimental Analysis of Behavior, 61,* 65–81.

Breier, B. H., Krägeloh, C. U., Thompson, N. M., Landon, J. G., Miles, J. L., Fraser, M., & Davison, M. (2005). Maternal nutrition during pregnancy influences learning and behavioural adaptation in offspring. *Pediatric Research, 58,* 1058.

Bronzino, J. D., Austin La France, R. J., Morgane, P. J., & Galler, J. R. (1996). Diet-induced alterations in the ontogeny of long-term potentiation. *Hippocampus, 6,* 109–17.

Davison, M., & Baum, W. M. (2000). Choice in a variable environment: Every reinforcer counts. *Journal of the Experimental Analysis of Behavior, 74,* 1–24.

Davison, M., & Baum, W. M. (2003). Every reinforcer counts: Reinforcer magnitude and local preference. *Journal of the Experimental Analysis of Behavior, 80,* 95–129.

Davison, M. C., & Hunter, I. W. (1976). Performance on variable-interval schedules arranged singly and concurrently. *Journal of the Experimental Analysis of Behavior, 25,* 335–345.

Davison, M., & Jenkins, P. E. (1985). Stimulus discriminability, contingency discriminability, and schedule performance. *Animal Learning and Behavior, 13,* 77–84.

Davison, M., & McCarthy, D. (1988). *The Matching Law: A research review.* Hillsdale, NJ: Erlbaum.

Davison, M., & Nevin, J. A. (1999). Stimuli, reinforcers, and behavior: An integration. *Journal of the Experimental Analysis of Behavior, 71,* 439–482.

DeBassio, W. A., Kemper, T. L., Tonkiss, J., & Galler, J. R. (1996). Granule cell generation in the hippocampal dentate gyrus. *Brain Research Bulletin, 41,* 379–383.

Elliffe, D., & Alsop, B. (1996). Concurrent choice: Effects of overall reinforcer rate and the temporal distribution of reinforcers. *Journal of the Experimental Analysis of Behavior, 65,* 445–463.

Herrnstein, R. J. (1961). Relative and absolute strength of response as a function of frequency of reinforcement. *Journal of the Experimental Analysis of Behavior, 4,* 267–272.

Landon, J., & Davison, M. (2001). Reinforcer-ratio variation and its effects on rate of adaptation. *Journal of the Experimental Analysis of Behavior, 75,* 207–234.

Lobb, B., & Davison, M. C. (1975). Performance in concurrent interval schedules: A systematic replication. *Journal of the Experimental Analysis of Behavior, 24,* 191–197.

Long, J. M., & Kesner, R. P. (1998). Effects of hippocampal and parietal cortex lesions on memory for egocentric distance and spatial location information in rats. *Behavioral Neuroscience, 112,* 480–495.

Luce, R. D. (1959). *Individual choice behavior: A theoretical analysis.* New York: Wiley.

Miller, H. L. Jr., & Loveland, D. H. (1974). Matching when the number of response alternatives is large. *Animal Learning & Behavior, 2,* 106–110.

Miller, J. T., Saunders, S. S., & Bourland, G. (1980). The role of stimulus disparity in concurrently-available reinforcement schedules. *Animal Learning & Behavior, 8,* 635–641.

Murrell, P. R. (1995). *Choice on three concurrent alternatives.* Unpublished Master's thesis, University of Auckland, Auckland, New Zealand.

Natapoff, A. (1970). How symmetry restricts symmetric choice. *Journal of Mathematical Psychology, 7,* 444–465.

Pliskoff, S. S., & Brown, T. G. (1976). Matching with a trio of concurrent variable-interval schedules of reinforcement. *Journal of the Experimental Analysis of Behavior, 25,* 69–73.

Schneider, S. M., & Davison, M. (2005). Demarcated response sequences and generalised matching. *Behavioural Processes, 70,* 51–61.

Vickers, M. H., Breier, B. H., McCarthy, D., & Gluckman, P. D. (2003). Sedentary behaviour during postnatal life is determined by the prenatal environment and exacerbated by postnatal hypercaloric nutrition. *American Journal of Physiology – Regulatory, Integrative and Comparative Physiology, 285,* R271–R273.

Woodall, S. M., Breier, B. H., Johnston, B. M., & Gluckman, P. D. (1996). A model of intrauterine growth retardation caused by chronic maternal undernutrition in the rat: Effects on the somatotrophic axis and postnatal growth. *Journal of Endocrinology, 150,* 231–242.