

*KEY-PECK PROBABILITY AND TOPOGRAPHY IN A
CONCURRENT VARIABLE-INTERVAL VARIABLE-INTERVAL
SCHEDULE WITH FOOD AND WATER REINFORCERS*

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The relation between variables that modulate the probability and the topography of key pecks was examined using a concurrent variable-interval variable-interval schedule with food and water reinforcers. Measures of response probability (response rates, time allocation) and topography (peck duration, gape amplitude) were obtained in 5 water- and food-deprived pigeons. Key color signaled reinforcer type. During baseline, response rates and time allocations were greater to the food key than to the water key, and food-key pecks had larger gapes and shorter durations. Relative probability measures (for the food key) were increased by prewatering and decreased by prefeeding. Deprivation effects upon topography measures were apparent only when food- and water-key pecks were analyzed separately. Food-key gape amplitudes increased with prewatering and decreased with prefeeding. The clearest effect occurred with prewatering. There were no consistent effects upon water-key gapes. The key color-reinforcer relation was reversed for 3 pigeons to determine how response topography was modulated during the transition from food- to water-key pecks. Reacquisition was faster for the probability than for the topography measures. Analysis of gape-amplitude distributions during reversal indicated that response-form modulation proceeded through the generation of intermediate gape sizes.

Key words: concurrent VI VI, response rate, time allocation, topography, reinforcer quality, deprivation, pigeon

Because the functional utility of a response is determined by both its form and its probability, the control of the response must involve modulation of both properties. For example, eating, drinking, grasping, grooming, and nest building in many avian species are similar in that all involve coordinated movements of the head and beak, but the responses are functionally distinguished by differences in the spatio-temporal organization of those movements (i.e., by topography). In fact, even the shaping of the pigeon's key peck involves the reinforcement of response topographies (e.g., a rapid, forceful, downward head movement) that, in interaction with the response transducer, will produce effective and reliable key displacements. Although much research in autoshaping has been devoted to analyzing response topography (as it relates to the stimulus substitution hypothesis; Woodruff & Williams, 1976),

most studies of learning have focused on the control of response rate, time allocation, or other probability measures. Relatively little is known about the variables that control response topography, and even less is known about the manner in which they interact with those that control response probability. Do such variables as reinforcer type and deprivation manipulations modulate both the frequency (probability) and topography of the response, what form does that modulation take, and what is its time course? The answers to these questions are particularly important for the analysis of behavior patterns, such as the pigeon's pecking, where the response is composed of identifiable components (e.g., LaMon & Zeigler, 1988) so that the same variable could have different effects upon different components of that response.

Answering these questions requires the separate measurement of response probability and topography, explicit control of reinforcement contingencies, and systematic manipulations of reinforcer properties. In previous studies (Allan & Zeigler, 1994; Ploog & Zeigler, 1996) both response strength (response rates and latencies, based on key pecks and gapes) and response topography

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(gape amplitude, i.e., interbeak distance) were simultaneously measured in the same subject. In the first phase of the present study, these measures were obtained during baseline responding under a simple concurrent variable-interval variable-interval (concurrent VI VI) schedule and after deprivation manipulations. Both food and water reinforcers were used, with key colors signaling reinforcer type. In the second phase of the study, the relationship between the keylights and the outcome (reinforcer type) was reversed.

The design of the study was intended to facilitate the gathering of data on both probability and topography within the same test situation. The use of food and water as reinforcers provided a qualitative manipulation involving two different types of consummatory response topography. It thus allowed us to replicate some aspects of Jenkins and Moore's (1973) classic study of the determinants of response form in a test situation that also provided data on response probability. The response-dependent procedure generated higher response rates than those obtained in our previous autoshaping studies. The use of discriminative stimuli (S^D ; keylights) as signals of the two reinforcer types retained some aspects of the stimulus-reinforcer relation that are present in autoshaping paradigms, between conditional stimulus (CS) and unconditional stimulus (US). In addition, the response-dependent concurrent schedule allowed the bird to choose freely between food or water reinforcers. (It could therefore titrate its own food- and water-deprivation levels, thus possibly keeping both food and water deprivation roughly at equilibrium.) The concurrent procedure also made it possible to examine the data in light of the extensive literature on choice (e.g., Herrnstein, 1970; Shurtleff, Warren-Boulton, & Silberberg, 1987). Specifically, this schedule permitted moment-to-moment assessment of the effects of manipulating deprivation levels (and by extension reinforcement value) upon measures of both probability (response rates, time allocations; e.g., Willis, van Hartesveldt, Loken, & Hall, 1974) and topography (gape amplitude, peck duration). It also enabled us to determine the extent to which the topography of the choice response is congruent with the outcome (reinforcer) signaled by the S^D or CS (e.g., Jen-

kins & Moore, 1973), that is, whether the bird's response topography reflected what might be called an expectancy (based upon its past history) with respect to the chosen outcome. The inclusion of a reversal condition allowed us to compare the rates at which response probability and topography are reacquired; these data relate to the hypothesis that response probability and topography may be affected by different classes of conditioning procedures.

The present study also provided data that are relevant to the problem of response-form modulation. Animals frequently shift from one behavior to another, using the same muscles to produce a variety of functionally distinct movement patterns (e.g., eating, drinking, preening, and singing movements in birds). Such *motor program switching* (Harris-Warrick & Marder, 1991) has primarily been studied in invertebrates. However, the observation (e.g., Jenkins & Moore, 1973) that ingestive and conditional responses in pigeons share many topographic features has made conditional pecking a useful preparation for studies of response-form modulation. Stimulus, reinforcer, and deprivation variables, which are typically confounded in consummatory responding, may be experimentally isolated in the conditioning preparation in order to examine their role in the determination of pecking response form.

The present study also extended a previous report on the modulation of conditional response form (LaMon & Zeigler, 1988), but incorporated several methodological improvements. These included a within-subject design to permit assessment of within-session effects and to control for possible response generalization (from consummatory responding to key pecking), the use of standardized food pellets to minimize variability in gape responses, and a gape measurement system that permitted continuous, high-resolution monitoring of gape amplitudes (Deich, Houben, Allan, & Zeigler, 1985). Moreover, the inclusion of a reversal condition allowed us to monitor the development of the new topographies associated with each of the keys during their reacquisition, thus providing a behavioral window on the modulatory process.

METHOD

Subjects

Eight experimentally naive French Mon-dain pigeons were housed in individual cages under a 12:12 hr light/dark cycle, with grit always available. They were reduced to 80% of their free-feeding weights and were maintained at their weights by provision of limited amounts of food and water during experimental sessions (conducted every other day) plus food supplements in the home cages. In addition, 1 hr after completion of each session, subjects were given unrestricted access to water for 2 hr.

Apparatus

Chamber. The experiment was carried out in a sound-attenuating enclosure, with additional sound masking by white noise. The enclosure contained an operant conditioning chamber, 40 cm in height with a wire-mesh floor (30.5 by 38.5 cm, elevated by 5 cm). The intelligence panel (front wall) and the rear wall were of sheet aluminum (0.12 cm thick) painted matte black. One side wall was of neutral-gray PVC (0.5 cm thick), and the other side wall and the ceiling were made of 0.5-cm clear Plexiglas. Three commercially available standard pigeon keys (2.5 cm diameter, BRS/LVE PPK-002), 20 cm above the mesh floor, 8 cm apart from the side walls, and with 7.5-cm center-to-center distance between keys, could be transilluminated with red or green 1-W bulbs (standard IEE 28-V 12-stimulus in-line projectors). A minimum of 0.18 N was necessary to trigger the key switch. The houselight consisted of two ceiling-mounted 2.8-W bulbs. Centered in the front panel, 5 cm above the floor, was an opening (9 by 10 cm) with access to a compartment (7 cm deep) for reinforcer delivery. The compartment was vertically divided in half. The left side was reserved for pellet delivery, and the right side was used for water delivery. In the center of the floor of each reinforcement compartment was a circular hole, 5 cm in diameter, that could be covered from below with a solenoid-operated watchglass. When the watchglass was operated, the compartment was illuminated by a 2.8-W bulb. When the food compartment was illuminated, a pellet dispenser delivered one spherical food pellet (Bioserv®) of 9.2-mm diameter (500

mg weight) onto the raised watchglass. When the water compartment was illuminated, a valve released 0.3 cc of water onto the raised watchglass. At the end of each reinforcement period, the watchglass was lowered, thereby disposing of any unconsumed water or pellets. Scheduling of experimental events, data collection, and subsequent data analysis were performed by a Macintosh IIci® computer (Apple), an I/O interface card with 12-bit analog-to-digital converter (Lab-NB®, National Instruments), and THINK C 6.0 (Symantec) software.

Recording of key-peck data. For response rates, key pecks to the left and right keys were recorded separately throughout each session. Time allocation to either response alternative was also based on the occurrence of key pecks. A peck to one key started a timer that accumulated time until a peck to the other key occurred. This peck started a second timer that accumulated time for the second key. In addition, the number of obtained food and water reinforcers was recorded. Both response rates and time allocation represent response probability (choice) measures (e.g., Domjan & Burkhard, 1993, p. 200), whereas peck duration and gape amplitude, described below, are two aspects of response topography.

Recording and definition of gapes. Gape (interbeak distance) was continuously recorded using a modification of a previously described magnetosensitive transducing system (Deich et al., 1985) for which a Hall-effect microchip and a small neodymium magnet were glued to the upper and lower beaks, respectively. The fine wires from the chip were held to the back of the pigeon's head by a small crocodile clip to avoid entanglement and were then plugged into a ceiling-mounted jack. The chip's continuous voltage output, which was proportional to beak opening, was digitized with the analog-to-digital converter at a 1-ms sampling rate. (The key-switch state, open or closed, was recorded in a similar manner to preserve information on the temporal relations between gapes and pecks, and to assess peck duration.) The gape-monitoring system was calibrated before each session by placing a tapered aluminum rod, with 2-mm gradations, between the beak tips to produce gapes increasing from 2 to 20 mm in 2-mm steps, and by recording the corre-

Table 1

Order of conditions, number of sessions, key color and reinforcer assignment, and deprivation state for 5 birds.

Session	Pigeon					Schedule
	P1	P2	P3	P4	P5	
Pretraining (food and water deprived)						
1-5	R-W ^a	G-W	R-F	R-F	G-W	Auto + FR 1 ^b
6-20	R-W	G-W	R-F	R-F	G-W	Auto + FR 1-3
21-35	R-W	G-W	R-F	R-F	G-W	FR 3
36-40	R-W	G-W	R-F	R-F	G-W	conc VI VI (10-45 s)
Baseline (food and water deprived)						
1-20	R-W	G-W	R-F	R-F	G-W	conc VI VI (45 s)
Single deprivation (food or water deprived)						
1-3	R-W(F) ^c	G-W(W)	R-F(W)	R-F(W)	G-W(F)	conc VI VI (45 s)
Recover baseline (food and water deprived)						
1-9	R-W	G-W	R-F	R-F	G-W	conc VI VI (45 s)
Reinforcement reversal (food and water deprived)						
1-25	R-F	G-F	—	R-W	—	conc VI VI (45 s)
Single deprivation (food or water deprived)						
1-3	R-F(W)	G-F(F)	—	R-W (F)	—	conc VI VI (45 s)
Single deprivation reversal (food or water deprived)						
1-3	R-F(F)	G-F(W)	—	R-W (W)	—	conc VI VI (45 s)

^a R = red, G = green, F = food, W = water, for the left key. The right key had the alternative color and was associated with the alternative reinforcer.

^b Auto = autoshaping; FR = fixed-ratio schedule of reinforcement.

^c (F) = food deprived only, (W) = water deprived only.

sponding digital values. For subsequent data analysis, an exponential curve was fitted to the points defined by these pairs of analog-digital values and then used to convert any observed digital value to its corresponding analog value (in millimeters). A gape response was defined as any beak opening whose amplitude first exceeded the beak resting position by 0.75 mm and then remained above this level for at least 5 ms. Resting position was defined as the most frequent gape-amplitude value for 1.5 s of the sampling period (i.e., the beak position before or between gape responses; cf. Ploog & Zeigler, 1996). Peak gape amplitude was defined as the maximum value during a key peck. Gape responses associated with key-switch closures were classified as food- or water-key gapes on the basis of which key was pecked. Gapes were recorded during all sessions for a maximum of 8 s before reinforcement and for 4 s during reinforcement. If the keylights were lit (interreinforcement interval) for less than 8 s, gapes were recorded for the entire duration.

Procedure

Prior to training, assignment to experimental conditions was counterbalanced across 8 birds. Three pigeons that failed to consume water or food reinforcers reliably were excluded from the experiment. Table 1 shows for the remaining 5 subjects the order of conditions, number of sessions, key color and reinforcer assignment, and deprivation state for pretraining and all experimental sessions.

Pretraining. All birds, water and food deprived, were first trained to eat the pellet (left compartment) or drink the water ration (right compartment) within 3 s of delivery. Several 30-min sessions were then conducted in which either water or a pellet was delivered in random order without a signal. (Most birds ate reliably before they drank from the hopper.) Subsequently, a modified autoshaping procedure (Brown & Jenkins, 1968) was in effect for 20 sessions as follows: After an intertrial interval (ITI) of 45-s mean duration (see Fleshler & Hoffman, 1962), either a red or green keylight was presented on the left

or right key. If no response occurred, the key-light (CS) terminated after 6 s and the 6-s US period began, during which either a pellet or water was delivered. If a key peck occurred, the CS was terminated immediately, and the US period was initiated (fixed-ratio [FR] 1 schedule). After five sessions, the ratio requirement was changed over 15 sessions from FR 1 to FR 3. For an additional 15 sessions, only the FR 3 requirement was in effect; that is, response-independent reinforcement was omitted. The autoshaping and FR 3 conditions were in effect for a total of 35 sessions, longer than required for simple pretraining, because those sessions represented a condition for a study unrelated to the present one. The last pretraining phase consisted of five concurrent variable-interval (VI) x -s VI x -s schedules, described below, with x being gradually changed from 10 s to 45 s, the final value for all subsequent experimental conditions.

General procedure: Simple concurrent schedule. For all sessions under the simple concurrent schedule, red and green keylights were simultaneously presented on the left and right keys. Scheduled contingencies were as follows: Two independent VI timers (Fleshler & Hoffman, 1962) on the left and right keys scheduled peck-dependent delivery of either one 0.3-cc ration of water or one 500-mg pellet. When a timer arranged an opportunity for reinforcement, a peck produced the reinforcer only if a changeover delay (COD) criterion had been fulfilled. The COD criterion required a minimum of two successive pecks to the same key separated by an inter-response time of at least 1 s, with only the second or subsequent pecks eligible for reinforcement (see Preston & Fantino, 1991). (Note that this COD requirement, even though shorter than usual, completely excluded the possibility of inadvertent reinforcement of changeover responses.) After reinforcer delivery, the hopper continued to operate for 12 s, during which the digitized gape data could be saved to the computer's hard disk and plotted to the screen. After the 12-s reinforcement period, the red and green keylights were presented again on the left and right keys, and a new reinforcement cycle began. The houselight was lit throughout a session except when a hopper was operated. Each session lasted until a combined total of

80 food and water reinforcers had been delivered.

Baseline. For 20 sessions, the concurrent VI 45-s VI 45-s schedule was in effect, arranging a choice between water and food reinforcers. The color/position/reinforcer correlation for each bird remained the same as during pretraining (Table 1). All birds were water and food deprived throughout.

Deprivation: Prefeeding or prewatering. For the next three sessions, with contingencies as under the baseline condition, Pigeons 1 and 5 were given ad lib water before the session (now food deprived only); Pigeons 2, 3, and 4 were given ad lib food before the session (now water deprived only). Prefeeding or prewatering was initiated at least 2 hr before the first single-deprivation session and continued for all subsequent single-deprivation sessions.

Baseline recovery. In order to recover their 80% free-feeding weights and to reestablish the standard water-deprivation level, baseline conditions were reinstated for nine sessions. Because the pigeons exhibited clear preference for the food outcome (choice proportion of approximately .80), the amount of each water reinforcer was increased from one to five 0.3-cc rations. (This permitted assessment of whether relative preference could be altered, but it had no obvious effect on performance.) The larger water reinforcers were given for the remainder of the experiment.

Reversal of reinforcer type. Two of the pigeons were shifted to a different, unrelated experiment. Only Pigeons 1, 2, and 4 continued to serve for the remainder of the experiment. For the next 25 sessions, the contingencies were identical to the previous ones except that the food or water outcome associated with each key was reversed. For example, as shown in Table 1, for Pigeon 1 pecks to the red key on the left (which had previously produced water) now produced food, whereas pecks to the green key on the right (which had previously produced food) now produced water.

Deprivation and deprivation reversal: Prefeeding or prewatering. For Pigeon 1, three sessions with free access to food in its home cage (now water deprived only) were followed by three sessions with free access to water (now food deprived only). Pigeons 2 and 4 were given three sessions with free water (now food de-

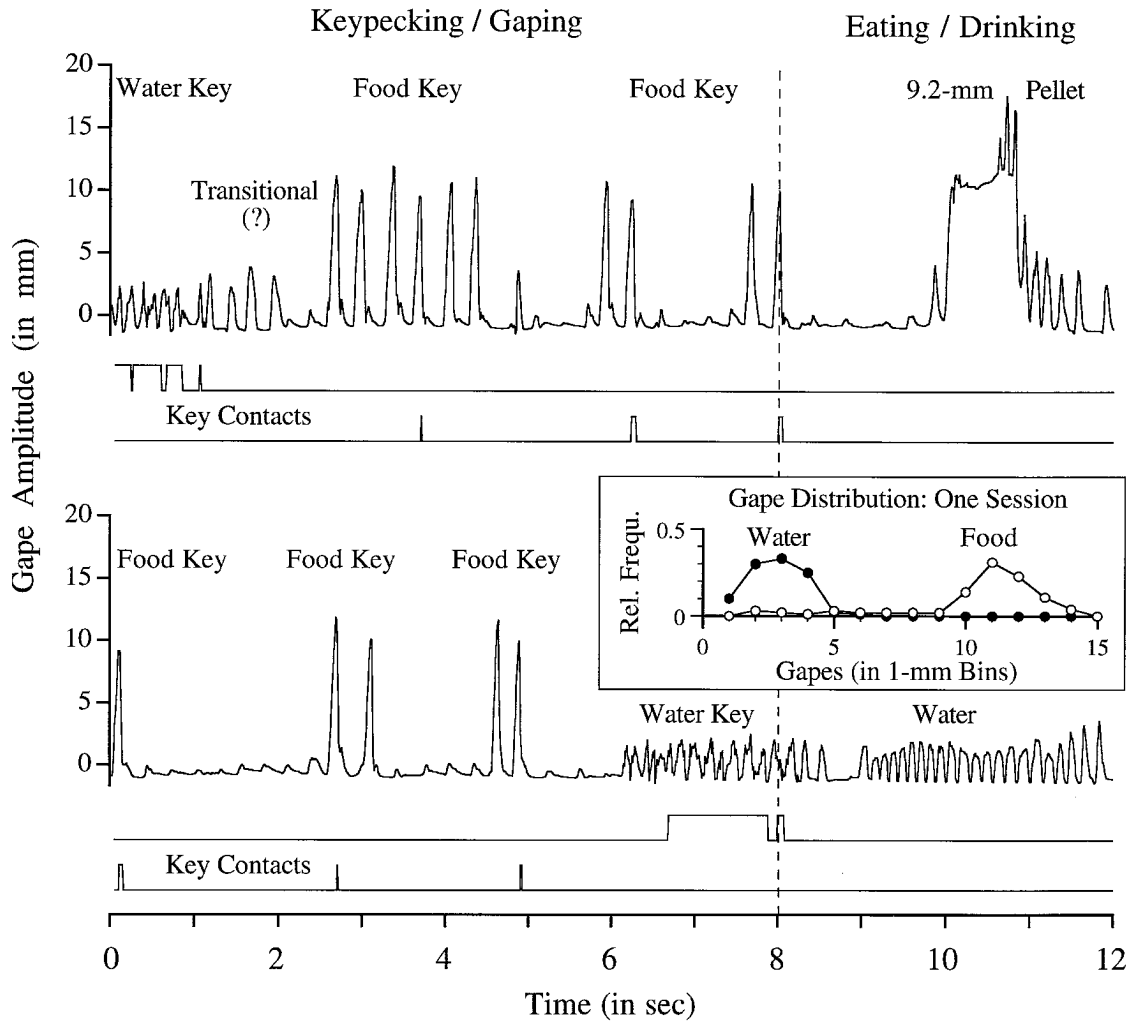


Fig. 1. A sample record of gape and key-peck responses over time produced by Pigeon 2 on two trials (top: food; bottom: water) during the 10th baseline session. The top trace in each graph shows variations in gape amplitude over time, and the two bottom traces indicate the times when either of the two keys was operated (high = switch closed). The record includes the last 8 s of the choice period (dotted vertical line) and the first 4 s of the reinforcement period (water or 9.2-mm pellet). The inset shows the food- and water-key gape distributions, arranged in 1-mm bins, for the entire session from which the two trial records were taken.

prived only) followed by three sessions with free food (now water deprived only).

RESULTS

To illustrate the type of observations on which subsequent analysis was based, Figure 1 presents data from Pigeon 2 on a trial with food outcome and a trial with water outcome. Note that gape responses could be assessed independently of key-switch closure. Moreover, a gape made in association with a spe-

cific (food or water) key-switch closure could be classified as a food- or water-related gape. Figure 1 illustrates some of the general findings of the experiment. First, across the trials the bird distributed its pecks to both the food and the water keys. Second, both gapes and key contacts made to the two keys were distinctly different in their topographies: Gapes associated with the food key were considerably larger than those associated with the water key, and pecks made to the food key were of shorter duration than those made to the

water key. Third, the topography of the choice response was congruent with the outcome (reinforcer) signaled by the keylight to which the peck occurred. Fourth, there was no overlap in the gape-amplitude distribution of food-key and water-key gapes. (This result held for 3 of the 5 birds [Pigeons 2, 3, and 5] in the baseline condition.) Fifth, water-key switch closures were associated with more gapes than were food-key switch closures. Sixth, there were many food and water gapes that were not associated with a peck to any key.

Response Probability and Topography under Baseline and Reversal

By the end of the baseline condition, the findings were quite consistent for all birds with respect to both probability and topography measures. Because there was considerable intersubject variability, all data were transformed into relative (normalized) measures. Figure 2 shows that more food than water reinforcers were produced, response rates to the food key were higher than to the water key, and more time was allocated to the food alternative than to the water alternative. Food pecks were characterized by larger gape amplitudes than water pecks (based on mean peak amplitudes while the key was pecked), whereas key-switch closures associated with water pecks had relatively longer durations than those of food pecks. (Note the inverse, but nevertheless consistent, relation between the peck-duration measure and the other four response measures.) In the reversal condition, the proportions were initially opposite to those at the end of the baseline condition because responding was still under the control of the previous contingencies. By the end of the reversal condition, however, all data were similar to those under baseline, indicat-

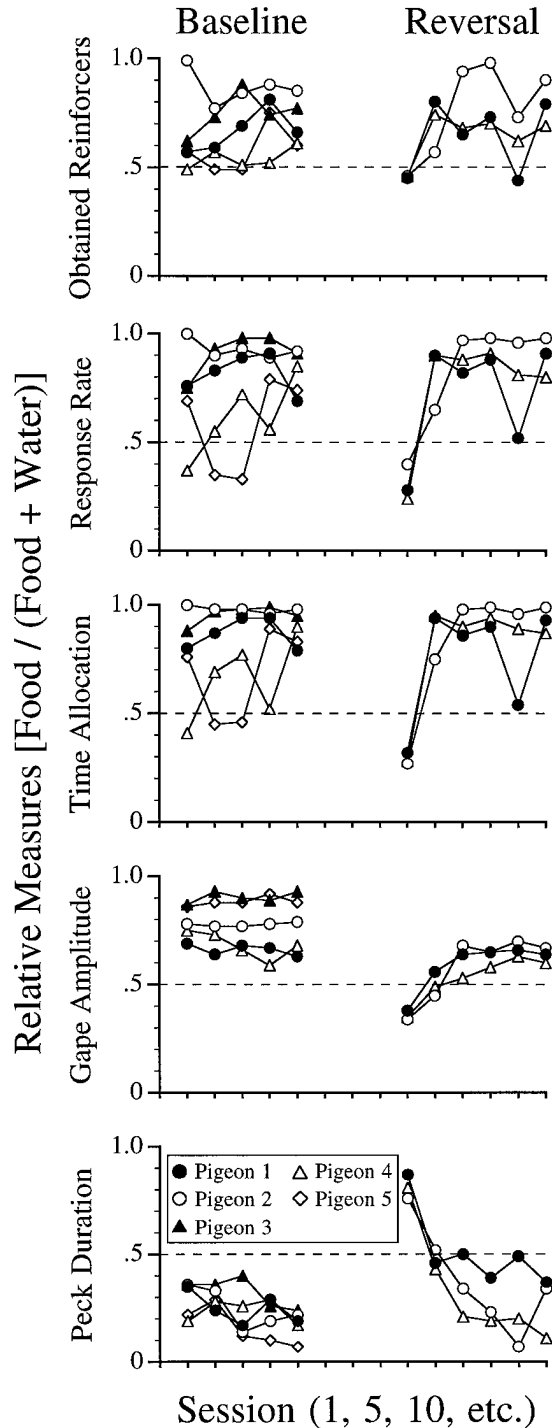


Fig. 2. Relative proportions of food-related to water-related responses for each of 5 pigeons (five symbols) using five response measures (five panels). Dotted horizontal lines indicate indifference. The data were taken from the first and every fifth session under the baseline and reversal conditions. The pigeons were under simultaneous food and water deprivation. For a few sessions in baseline, when sampling failed, data were replaced by data from a preceding session. The absolute measures underlying these relative measures are included in the Appendix.

ing reacquisition of the original response probabilities and topographies. With one exception (Pigeon 1, Session 20, probability measures), behavior was stable by the 10th reversal session.

Figure 3 shows the time course of such reacquisition under reversal, for each of the two probability (response rate and time allocation) and two topography (gape amplitude and peck duration) measures. The point at which each function crosses the .5 line indicates a switch from water- to food-typical behavior. These crossovers occurred at distinctly different points for the probability measures than for the topography measures. For response rates and time allocation, the switch took place between Sessions 1 and 2 for Pigeons 1 and 4 and between Sessions 2 and 3 for Pigeon 2; for gape amplitude and peck duration, it took place after Session 4 for Pigeon 1, after Sessions 5 and 6 for Pigeon 2 for the two topography measures, respectively, and after Sessions 5 and 3 for Pigeon 4 for the two topography measures, respectively. Thus, without exception, reversal occurred earlier for the probability than for the topography measures.

Gape-Amplitude Distributions under Baseline and Reversal Conditions

Figure 4 presents relative frequency distributions of gape amplitudes for the 5 subjects tested under the baseline condition. Pigeons 1, 2, 3, and 5 exhibited clearly separate gape-amplitude distributions for the food and water keys. For those birds, Pigeon 1 had the most, and Pigeon 5 the least, overlap in distributions. Pigeon 4 produced gape-amplitude distributions for the water key that were similar to those of the other 4 birds; but unlike those of the other birds, its food-gape distributions were flat, covering a wide range, and with most gapes occurring at low amplitudes. Despite intersubject differences, however, the specific individual characteristics of the distributions remained stable for each bird throughout the baseline condition.

Figure 5, similar to Figure 4 in arrangement, shows gape-amplitude distributions for the 3 subjects under the reversal condition. For Pigeons 1 and 2 the results are very clear: The gape amplitudes associated with the food and water keys were initially separated, with large gapes occurring to the water key (ex-

emplifying the persisting effects of the pre-reversal contingencies). Throughout the reversal condition, the modes of the water-gape distributions decreased while the modes of the food-gape distributions increased until two distinct distributions were obtained again at the end of the reversal condition. At this stage, as under baseline, gape amplitudes associated with the food key were large, whereas water-associated gapes were small. Session 5 was the midpoint of this transitional process, when both distributions overlapped maximally. This was also about when gapes with intermediate amplitudes occurred; such amplitudes were rare or absent before reversal for either the food or water key. Pigeon 4 showed different results to the extent that both distributions were never as clearly separated as those of the other 2 birds. At the end of reversal, however, Pigeon 4's gapes associated with the water key were also small and gapes associated with the food key tended to be large. Thus, Pigeon 4, too, exhibited reacquisition of outcome-specific topography after completion of the reversal condition.

Response Probability and Topography with Deprivation Manipulations

The baseline and reversal conditions were conducted with subjects maintained under simultaneous food and water deprivation. The deprivation levels were then manipulated by prefeeding (water deprived only) or by prewatering (food deprived only). Figure 6 shows the effects of this manipulation upon the response probability and topography measures. The five response measures are plotted as differences in the proportional measures (pooling food- and water-related behavior, similar to the proportions reported in Figure 2) between the last session of the previous condition and a given session with either prefeeding or prewatering. To the extent that the manipulation produced effects congruent with the deprivation condition, hatched bars should point upwards, and open bars should point downwards. With few exceptions, exactly this pattern was obtained for the probability measures. However, the two topography measures (pooling water- and food-key responses), which were included to facilitate comparison to the probability measures, yielded negligible or inconsistent changes for all birds under all conditions.

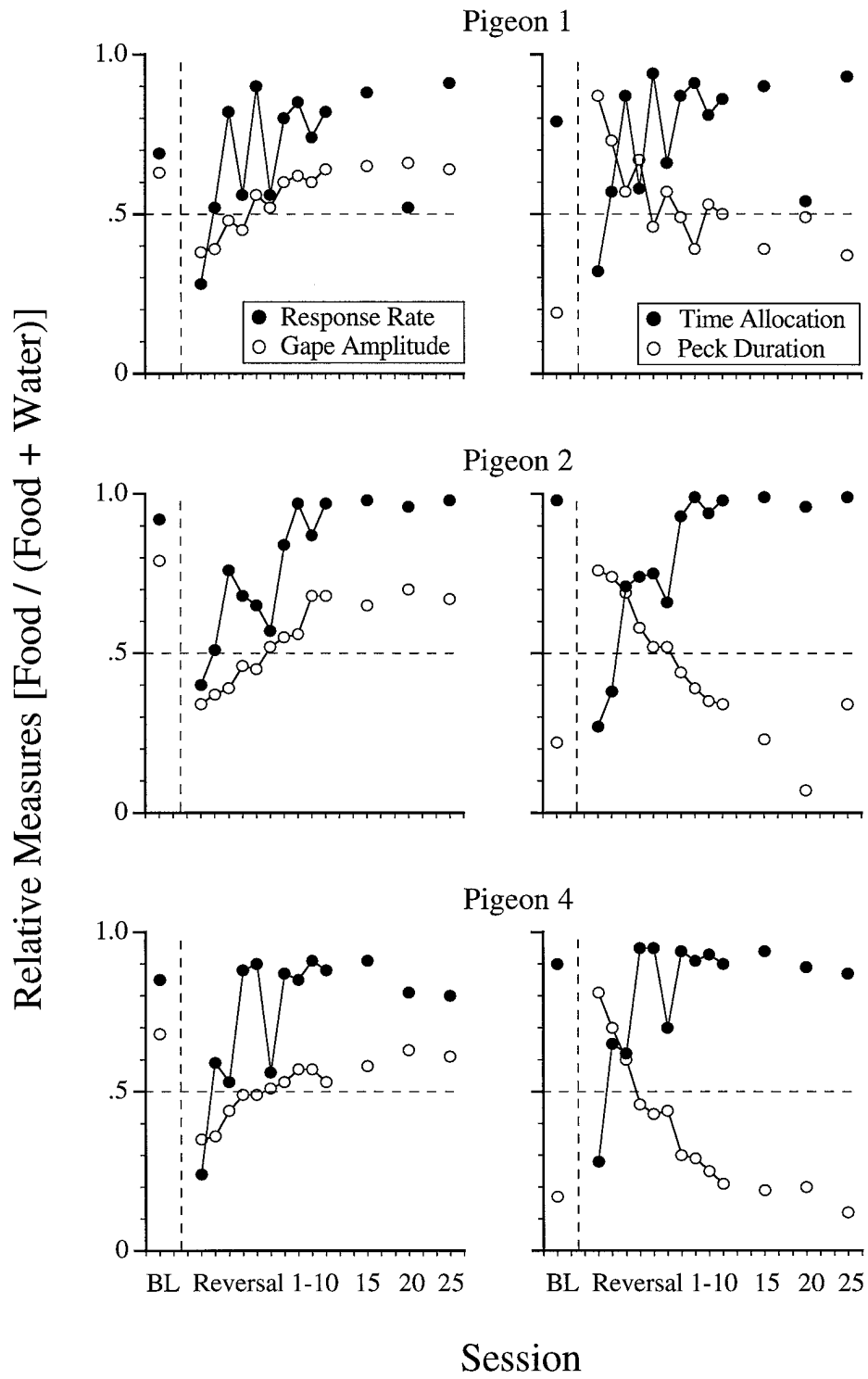


Fig. 3. Probability and topography measures for Reversal Sessions 1–10, 15, 20, and 25. Data from the last baseline session (BL) serve as reference points. The intersections with the dotted horizontal lines (indifference) indicate the points at which individual birds switched from water-typical to food-typical behavior.

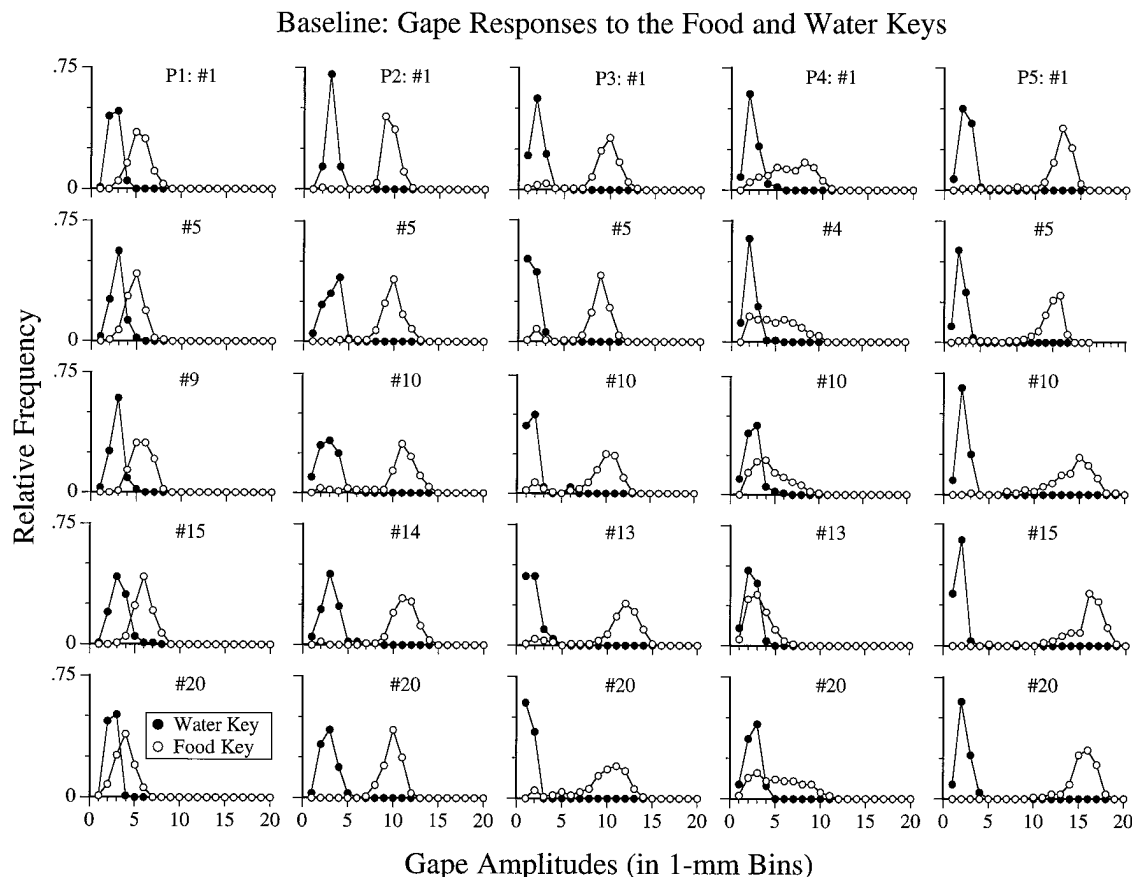


Fig. 4. Frequency distributions of gape amplitudes, in 1-mm bins, for pecks made to the food key (open circles) and water key (filled circles), for 5 birds (in columns) during the first and every fifth session (in rows) of baseline. For a few sessions, when sampling failed, data were replaced by data from a preceding session.

To clarify these findings, the data were separated with respect to food and water keys. The results of this analysis, presented in Table 2, indicate that deprivation had measurable effects upon the absolute mean gape amplitudes (in millimeters). The table compares data obtained under combined food and water deprivation for the final session of the acquisition ($n = 5$) or reversal ($n = 3$) conditions with those made following prefeeding (water deprivation only) or prewatering (food deprivation only). The relevant comparisons are between the amplitudes under combined food and water deprivation (lightface numbers) and those obtained under either water deprivation (*italic numbers*) or food deprivation (**boldface numbers**). Prewatering had no consistent effect upon the gape amplitude of either food or water key

pecks, the effects being equally divided (five of ten cases) between increased and decreased gapes. In contrast, water deprivation was associated with decreased gape amplitudes for pecks made to both the food and water keys in 11 of 12 cases.

Figure 7 extends this analysis by examining the manner in which deprivation manipulations affected the distributions of gape amplitudes for each key. The relevant data are the shifts in gape-amplitude modes relative to their previous values under the baseline or reversal conditions (indicated by dotted vertical lines). For distributions of food-key gapes, the effects were clear in eight of eleven cases: in six of six cases, prefeeding lowered the mode of the food-gape distribution (i.e., the open-circle distributions shifted to the left relative to the right dotted line); prewa-

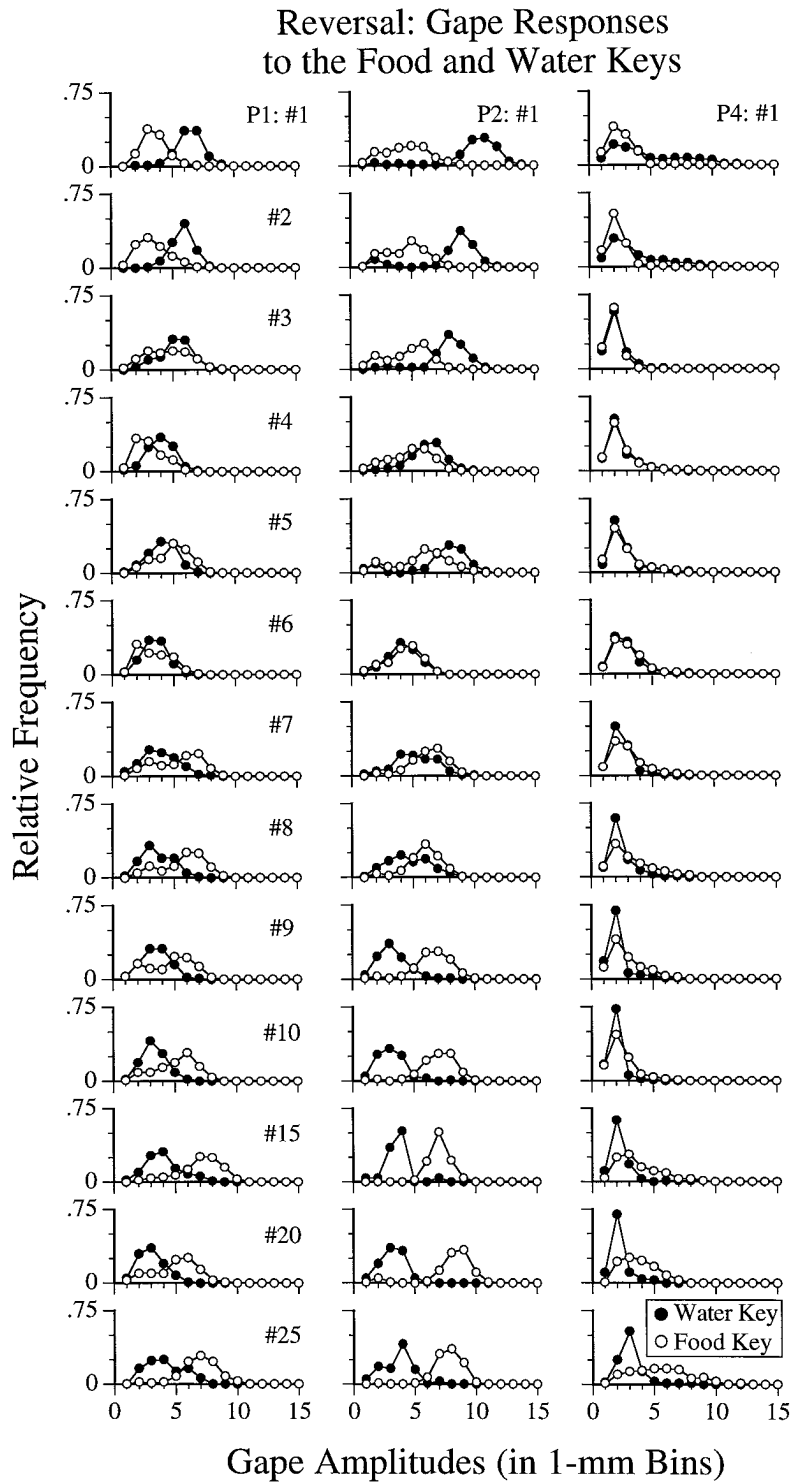


Fig. 5. Frequency distribution of gape amplitudes for pecks made to the food key (open circles) and water key (filled circles), for 3 birds during Reversal Sessions 1–10, 15, 20, and 25.

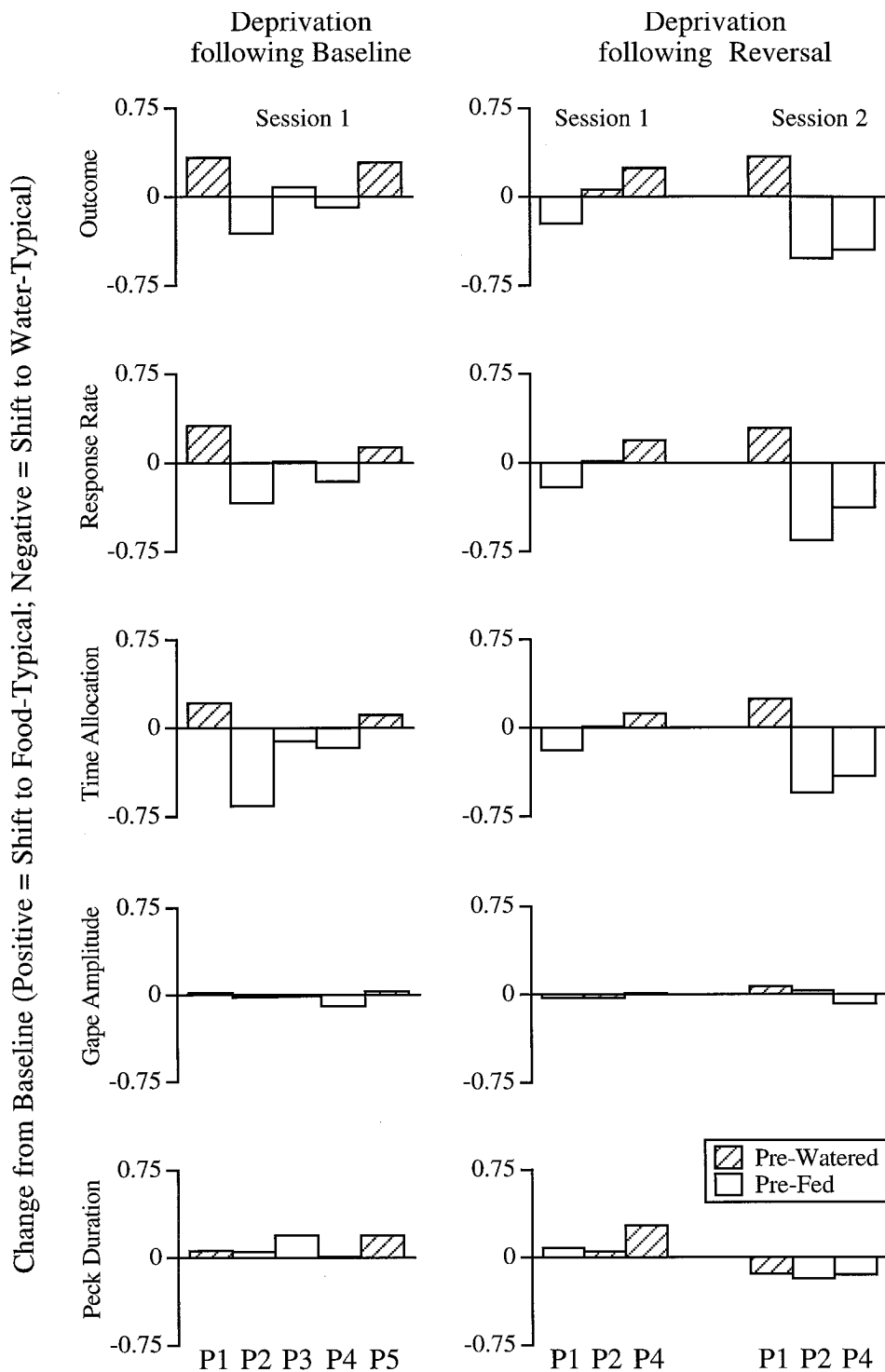


Fig. 6. Effects of prefeeding (open bars) or prewatering (hatched bars) on relative changes from the baseline (one session for each of 5 birds) and reversal conditions (two sessions for each of 3 birds). The lengths of the bars represent difference scores between the proportions obtained under the last session of the baseline or reversal condition and the first session with deprivation manipulation. Positive changes indicate a shift toward food-typical behavior; negative changes indicate a shift toward water-typical behavior.

Table 2

Mean gape amplitudes (in millimeters) associated with pecks to the food and water keys for the last session for 5 birds under baseline and for 3 birds under reversal, and for the single-deprivation sessions.

Pi-geon	Key	Baseline	Single deprivation	Reversal	Single deprivation	Single deprivation
1	Food	3.20	5.89	6.49	<i>5.04</i>	6.44
	Water	1.92	3.11	3.58	<i>3.17</i>	3.00
2	Food	9.43	<i>5.66</i>	7.27	8.40	<i>4.89</i>
	Water	2.53	<i>1.68</i>	3.58	4.66	<i>2.38</i>
3	Food	9.31	<i>8.20</i>	—	—	—
	Water	0.67	<i>0.72</i>	—	—	—
4	Food	5.11	<i>2.85</i>	4.69	4.46	<i>1.73</i>
	Water	2.39	<i>2.04</i>	3.07	2.87	<i>1.54</i>
5	Food	14.69	14.13	—	—	—
	Water	2.00	1.48	—	—	—

Note. Numbers in boldface refer to gape amplitudes under food deprivation; numbers in italics indicate gape amplitudes obtained under water deprivation.

had no apparent effect in three of five cases. In other words, the birds produced smaller food gapes when they were water deprived but not hungry, and sometimes produced larger food gapes when they were food deprived but not thirsty. In contrast, the deprivation manipulations had no consistent effect on the distribution of water gapes; that is, the modes of the filled-circle distributions did not shift in an orderly fashion with respect to pre-feeding or prewatering. (These findings, which are based on gape-amplitude modes, when analyzed according to key type instead of deprivation type are consistent with the data in Table 2, which are based upon gape-amplitude means. Pooling food- and water-gape measures as in Figure 6 may therefore have masked the effect of the deprivation manipulations on response topography.)

DISCUSSION

tering either increased the modes of the food-gape distributions (i.e., the open-circle distributions shifted to the right relative to the right dotted line) in two of five cases or

The present study examined the relation between variables that control the probability and topography of key pecking and described the manner in which such response topog-

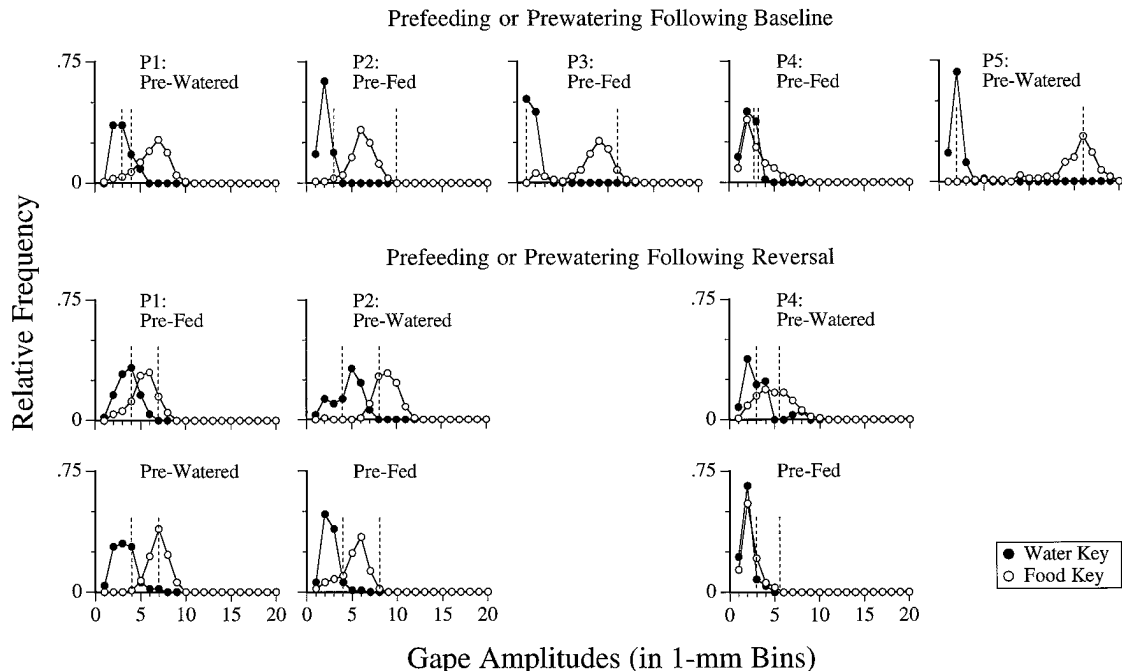


Fig. 7. Effects of deprivation manipulations upon the frequency distributions of gape amplitudes for pecks made to the food key (open circles) and water key (filled circles), following baseline (one session, 5 birds) or reversal (two sessions, 3 birds). Dotted vertical lines serve as reference points by indicating the modes of the last baseline or reversal session for the water key (left line) and food key (right line).

raphy is modulated by reinforcer properties and deprivation manipulations. Our findings also have implications for studying choice behavior, because they indicate the extent to which standard choice measures (response rate and time allocation) may be congruent with response topography.

Response Probability and Topography as a Function of Reinforcer Type

Both the probability and the topography of key pecking varied systematically with the type of reinforcer. Although the birds were both food and water deprived, response rates and time allocations indicated a significant preference for the key that signaled food. These findings are consistent with those of Willis et al. (1974), who used a similar paradigm in a study of lever pressing by rats. Furthermore, the topography of pecks to the food and water keys differed substantially in gape amplitude and peck duration (Figures 1, 2, 3, 4, and 5). Not only did the gapes of pecks to the food key tend to be substantially larger than those made to the water key (range for food, 2.9 to 14.9 mm; range for water, 0.6 to 3.1 mm), but for a given subject the absolute values of both gape types were quite consistent from session to session. These results, obtained with a within-subject design, confirm and extend those from previous studies from Zeigler's laboratory (Allan & Zeigler, 1994; LaMon & Zeigler, 1988).

Consistent differences between the duration of food and water key pecks have been previously noted (e.g., Jenkins & Moore, 1973; Spetch, Wilkie, & Skelton, 1981), and its simplicity of instrumentation recommends duration as a possible topography measure. However, LaMon and Zeigler (1988), using sophisticated instrumentation, failed to find such differences. They noted that contact duration, as measured in the typical key-pecking situation, reflects a complex interaction between the physical properties of the key (especially its trigger force) and the topographic features of the response (see also Ploog & Zeigler, 1996). The possibility of artifacts related to such interactions suggests the need for caution in using contact duration as a measure of key-peck topography.

Somewhat similar considerations apply to interactions between probability and topography measures and the definition of a re-

sponse unit when using key-peck-based choice measures (e.g., Herrnstein, 1970). In the present study, response rates and time allocation indicated that food was more reinforcing than water (relative response rates for food were about .80; relative time allocations were about .90). These results were unexpected because we assumed that the birds would switch between water and food until both deprivation levels came to be titrated at equilibrium (making water and food equally reinforcing), probably during the later part of a session. The apparent preference for food was even more surprising given the severity of water deprivation (about 44 hr), in contrast to rather moderate food deprivation (80% ad lib).

Subsequent analysis revealed that the strong apparent preference for food in the present study may be an artifact of the properties of the standard pigeon key that bear on its ability to detect key pecks. Although birds made more key pecks to the food key, the number of gape responses per key-switch closure was substantially greater (about 3:1) for the water key than for the food key (1:1). Had the response unit been a single gape response rather than a single key peck, or had the key switch been more sensitive to small beak movements, relative response rates might have been closer to .50 (indifference). Similar interactions may be present even in studies that involve a choice between different amounts of food, because food amount alone may also affect response topography (Ploog & Zeigler, 1996). Furthermore, in the present study, deprivation manipulations designed to change incentive value (similar to the effects of food amount or delay to food) affected the amplitude of gapes associated with the food key independently of their effects on the water key. Thus, relative response rates reflect an interaction among the topography of the response, the trigger characteristics of the key, and the definition of the response unit. (Note that this holds true even if both water and food keys are identical in their trigger properties, so that counterbalancing position does not solve the problem.)

Finally, an observation during the present study argues for caution in the use of response rates (and, by extension, time allocation) as a measure of reinforcement value. We observed that prefed birds continued to

peck the food key, indicating preference for food, but they failed to consume the pellet. This suggests, first, that key pecks may not accurately reflect unconditional reinforcement value; second, devaluation of a food reinforcer (by satiation) may not immediately change the evocative effect (conditional reinforcement value) of the associated S^D (key-light signaling a specific reinforcer). Gape-rate measures would have been equally problematic, because there were at least as many gape responses as key pecks under these conditions. Our observation may be interpreted in the light of the suggestion that behavior in the conditioning situation comprises a behavioral chain (orientation, approach, neck movement, head transport, coordinated beak movements, consumption of the pellet). Williams, Ploog, and Bell (1995) showed that devaluation (by extinction) had differential effects depending on the position of a link in the chain. In their study, devaluation affected response rate in the middle link more often and sooner than in the initial link. If key pecking is considered to be an early link in the chain and consummatory responses are considered to be a late link in the chain, the persistence in pecking despite low primary reinforcer value may reflect devaluation (prefeeding) effects on the consummatory (late) link, but not on the pecking (early) link. (Nevin, Mandell, & Yarensky's, 1981, interpretation in terms of resistance to change predicts larger changes in earlier than in later links. They found evidence of greater persistence in the terminal links of chains than in the initial links; these findings are not consistent with the present analysis.)

Effects of Deprivation and Reversal Manipulations on Probability and Topography Measures

As Jenkins and Moore (1973) pointed out, the design of the typical autoshaping experiment implicitly confounds reinforcer type and deprivation state as determinants of conditional pecking response form. Using observer ratings rather than direct measures of topography, they carried out several experiments to dissociate the two variables and concluded that the resemblance between auto-shaped and consummatory responses does not require "the dominance of a deprivational state appropriate to the reinforcer" (p.

170). Their data certainly seem to be consistent with this conclusion, because deprivation manipulations had relatively small and graded, rather than marked and dichotomous, effects upon observer ratings of response form. However, close inspection of the published ratings (Experiments 2 and 3) indicates that deprivation manipulations did affect topography slightly, producing a greater spread of ratings that reflects the appearance of intermediate ratings and reduces the reported differences between peck types.

Deprivation effects in the present study were assessed using prefeeding and prewatering manipulations to shift the relative value of food and water reinforcers in subjects that had previously been maintained under combined food and water deprivation. The effects of these manipulations on probability measures (greater values for food-related than for water-related behavior following food deprivation, and vice versa) were consistent with those reported by Willis et al. (1974). Deprivation effects on topography measures (not assessed by Willis et al.) were not apparent when relative measures were used, but analysis of the data separated by food and water keys indicated both the presence of such effects and an asymmetry with respect to their action. When based on mean gape amplitudes (Table 2), prewatering (food deprivation) had no effect on gapes to either key; prefeeding (water deprivation) was associated with a consistent reduction in the mean gape of pecks to both food and water keys. When based on modes (Figure 7), prefeeding and prewatering had an effect on food-related but not on water-related gapes. Because both manipulations shift the relative values of the reinforcers, the differing results of the two analyses are puzzling. Although we have no satisfactory explanation for these inconsistencies, our findings, in contrast to those of Jenkins and Moore (1973), demonstrate that deprivation state does modulate response topography. The inconsistencies between their results and ours (i.e., whether deprivation has an effect on response topography) may be due to procedural differences. (They tested deprivation effects under extinction, not by prefeeding or prewatering.)

The control of response form by deprivation manipulations and by the keylights (reversal) involved markedly different time

courses. Deprivation effects on both probability and topography were immediate, being evident during the first test session following the manipulation (Figure 6, Table 2, Figure 7). In contrast, the effects of the reversal manipulation became evident only after about two sessions of reacquisition for the probability measures and only after an even longer period for the topography measures (Figures 3 and 5). Indeed, for 2 of the 3 subjects, the final values of gape for pecks to the food key remained below their baseline mean for most of the reversal sessions.

Such differences in the time course of reacquisition of probability and topography measures might suggest that modulation of key-peck probability and key-peck topography results from different kinds of contingencies. (For example, Nevin, Tota, Torquato, & Shull, 1990, found compelling evidence that operant and Pavlovian contingencies may co-exist in an operant situation, and that they can have independent effects on different aspects of behavior.) In our study under the reversal condition, the topography measures lagged behind the probability measures. Assuming that topography is determined by Pavlovian contingencies (as is suggested by autoshaping studies in which reinforcer-specific topographies were obtained without explicit response-dependent contingencies; e.g., Allan & Zeigler, 1994; Jenkins & Moore, 1973; Ploog & Zeigler, 1996), this lag suggests that Pavlovian contingencies require more time than operant contingencies to affect the response measures. However, this conclusion is not supported in view of our findings that prefeeding and prewatering had an instantaneous effect on both measures (i.e., there was no difference in time course). Like the reversal contingencies, the deprivation manipulations presumably affected both the operant (response-reinforcer) and Pavlovian (stimulus-reinforcer) contingencies by changing the value of the reinforcer. Consequently, a lag between the topography and probability measures should have been observed again. However, the instantaneousness of the effect of the deprivation manipulations indicated that the effect of a change in reinforcer value did not depend on *any* of the prevailing contingencies (see below), and that therefore a difference in time course between operant and Pavlovian contingencies

should not have been expected in the first place with the deprivation manipulations.

Another reason for different rates at which reversal and deprivation manipulations took effect may be that the former involves conditioning processes (relearning of the current contingencies), whereas the latter involves an unconditional change of reinforcer value similar to the effects produced by the devaluation procedures used by Rescorla and his colleagues (e.g., Colwill & Rescorla, 1985). Such devaluation procedures are sometimes said to alter associations that involve the representation of the reinforcer, and the effects are assumed to be instantaneous.

The presence in our experimental design of both response-reinforcer and stimulus-reinforcer contingencies may have sharpened the differences between reacquisition times for probability and topography measures. However, the inference from different acquisition rates to different associative processes is not necessarily compelling. The measures used to define probability and topography in this study (pecks and gapes) reflect the operation of two different effector systems (neck and jaw, respectively). It has been repeatedly demonstrated that the two components may be experimentally dissociated, and that each may be brought under the associative control of either stimulus-reinforcer or response-reinforcer contingencies (Allan & Zeigler, 1994; Deich, Allan, & Zeigler, 1988; Lucas, Vodraska, & Wasserman, 1979; Mallin & Delius, 1983; Remy & Zeigler, 1993). However, although such dissociation may be demonstrated under laboratory conditions, it is probably the case that the acquisition of distinct response forms with variable probabilities involves the operation, in parallel, of both response-reinforcer and stimulus-reinforcer contingencies (e.g., Balsam, Deich, & Hirose, 1992, p. 32).

Mechanisms of Pecking Response Modulation

Response topography may be modulated by both deprivation and reversal manipulations, and our data clarify the processes that mediate these effects. Food deprivation increased the relative proportion of large food-key gapes; water deprivation increased the relative proportion of small food-key gapes. This shift in the distribution was immediate, being evident in the very first test session. In contrast, the effects of reversal were seen over

a relatively prolonged period and involved the generation of new response forms to each of the predictive stimuli (keylights).

The manner in which this takes place provides an interesting behavioral test of some current theoretical accounts of response-form modulation. One such account views the generation of distinctive species-typical response forms (e.g., eating and drinking) as reflecting the selective activation of preorganized neural circuits that mediate fixed movement patterns. A second account postulates single multifunctional circuits whose continuous modulation generates a variety of functionally distinct movement patterns. The first account suggests that regardless of how causal variables are manipulated, response topographies should fall into distinct classes without intermediate forms, whereas the second envisions the modulation of the response across a topographic continuum that includes intermediate forms. The first account was implicit in the *learned-release hypothesis* (Woodruff & Williams, 1976), which postulated the redirection of species-typical action patterns from the ingestive stimulus to the response key to account for the similarity of conditional and unconditional response forms. Evidence supportive of the second account was provided by an earlier study that examined response topography during a controlled transition between two different forms of the conditional key peck (LaMon & Zeigler, 1988). In the present study, as in that earlier study, the development of new conditional response forms to the keylights involved a continuous process. This was evident in particular under the reversal condition (Figure 5), when intermediate gape amplitudes emerged that were relatively infrequent or even absent under the baseline condition. Moreover, this finding, at the behavioral level, is consistent with a recent physiological analysis that related jaw muscle activity to eating and drinking response topography in the pigeon (Bout & Zeigler, 1994a, 1994b). This analysis showed that the substantial differences in gape amplitude and kinematic pattern that distinguish eating and drinking reflect primarily slight differences in the timing relations of the ensemble of opener and closer muscles.

Control of Response Form: Cognitive Versus Associative Accounts

Using peck force as a measure of response form, Stanhope (1992) found differences be-

tween the force of food- and water-reinforced key pecks during first-order but not second-order conditioning in pigeons. Based upon this and earlier studies of conditional response topography that involved reinforcer reevaluation (e.g., Davey & Cleland, 1982; Stanhope, 1989), Stanhope argued that the similarities between the form of the conditional response and the consummatory response reflects mediation of the conditional response by "information encoded in the representation of the US" (1989, p. 320). This account assumes that exposure to a stimulus associated with a specific outcome produces an internal representation of that stimulus that encodes outcome-specific information (also see Colwill & Rescorla, 1985). This cognitive interpretative language might be applied to the effects of the simple concurrent schedule of the present study. A representation seems to account for the observed relation among deprivation state, conditional pecking response form, and probability with respect to the response key. In cognitive terminology, the representation would mediate both what might be called an *intention* (i.e., an increase in the probability of pecking for a particular reinforcer) and what might be called an *expectancy* (i.e., selection of a response form appropriate to the signaled reinforcer) prior to reinforcer delivery. The consistent differences between the form of food and water pecks, as well as the effects of the deprivation manipulations on response topography, are in agreement with the common understanding of a mediating internal representation.

However, like the stimulus-substitution and the learned-release accounts, the cognitive account fails to predict, parsimoniously, either the specific differences or the similarities observed in quantitative comparisons between forms of consummatory pecking and key pecking (Allan & Zeigler, 1994; LaMon & Zeigler, 1988; Ploog & Zeigler, 1996). Moreover, in its strongest form this account predicts a high degree of congruence between the probability and topography measures. That is, if the pigeon chooses water rather than food (as shown by its response rate and time allocation), then the form of its key-pecking response should be congruent with that choice. During the reversal component of our study, such congruence was lacking or was incomplete for many sessions. This dissociation among measures of choice and to-

pography suggests that the direction, rate, and form of the conditional response are not evoked indirectly by some unitary central representation of the unconditional stimulus but reflect the formation of associations among the stimulus and response ensembles that are present during conditioning (Holland, 1984). The specific relations involved remain to be identified.

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APPENDIX

The absolute data underlying the relative measures presented in Figures 2, 3, and 4 according to the two reinforcer outcomes (food and water): number of obtained reinforcers, response rates, time allocation, mean gape amplitude, and mean peck duration for each individual bird, for the first and every fifth session of the baseline, reversal, and deprivation manipulation conditions.

Condition	Session	P1		P2		P3		P4		P5		
		Food	Water	Food	Water	Food	Water	Food	Water	Food	Water	
Number of obtained reinforcers												
Baseline	1	46	34	79	1	50	30	39	41	46	34	
	5	47	33	62	18	58	22	43	37	39	41	
	10 ^a	60	20	67	13	70	10	41	39	39	41	
	15 ^b	65	15	55	25	68	12	43	37	60	20	
	20	53	27	68	12	62	18	49	31	48	32	
Single deprivation	1 ^c	79	1	43	37	68	12	42	38	71	9	
Reversal	1	36	44	37	43	—	—	37	43	—	—	
	2	41	39	37	43	—	—	43	37	—	—	
	3	58	22	48	32	—	—	41	39	—	—	
	4	42	38	47	33	—	—	64	16	—	—	
	5	64	16	46	34	—	—	59	21	—	—	
	6	42	38	42	38	—	—	42	38	—	—	
	7	61	19	58	22	—	—	67	13	—	—	
	8	64	16	72	8	—	—	55	25	—	—	
	9	49	31	55	25	—	—	55	25	—	—	
	10	52	28	75	5	—	—	54	26	—	—	
	15	58	22	78	2	—	—	56	24	—	—	
	20	35	45	58	22	—	—	50	30	—	—	
	25	63	17	72	8	—	—	55	25	—	—	
	Single deprivation	1	45	35	77	3	—	—	74	6	—	—
	Single deprivation reversal	1	70	10	38	42	—	—	41	39	—	—
Number of responses per session												
Baseline	1	1,531	485	1,812	6	1,182	389	1,113	1,871	1,256	552	
	5	2,307	468	2,027	228	2,123	172	2,371	1,160	399	726	
	10 ^a	2,021	241	1,717	138	2,785	71	3,018	1,162	454	922	
	15 ^b	2,852	282	2,549	318	3,427	65	3,128	1,132	815	220	
	20	1,004	444	1,464	135	1,915	199	3,454	591	1,319	455	
Single deprivation	1 ^c	1,773	5	911	669	1,380	116	1,922	873	671	100	
Reversal	1	776	1,982	1,275	1,948	—	—	920	2,901	—	—	
	2	1,387	1,260	1,618	1,568	—	—	2,347	1,641	—	—	
	3	2,473	550	2,215	708	—	—	1,971	1,765	—	—	
	4	1,336	1,041	2,673	1,258	—	—	2,544	346	—	—	
	5	3,490	386	2,030	1,077	—	—	3,190	356	—	—	
	6	1,459	1,143	1,787	1,356	—	—	2,166	1,668	—	—	
	7	3,126	784	2,953	548	—	—	2,854	417	—	—	
	8	3,517	613	3,456	120	—	—	3,121	561	—	—	
	9	2,397	863	2,510	367	—	—	3,763	394	—	—	
	10	2,798	605	3,621	112	—	—	2,791	398	—	—	
	15	3,643	515	4,150	67	—	—	2,827	281	—	—	
	20	1,341	1,240	3,398	131	—	—	2,459	586	—	—	
	25	3,507	342	4,013	76	—	—	1,822	445	—	—	
	Single deprivation	1	2,426	1,055	3,524	31	—	—	3,608	53	—	—
	Single deprivation reversal	1	4,492	177	1,213	1,534	—	—	1,439	909	—	—

APPENDIX

(Continued)

Condition	Session	P1		P2		P3		P4		P5		
		Food	Water	Food	Water	Food	Water	Food	Water	Food	Water	
Time allocation (in minutes) per session												
Baseline	1	28.1	7.1	53.5	0.1	30.3	4.3	12.3	17.4	25.0	7.9	
	5	30.6	4.6	44.3	1.0	39.9	1.1	23.5	7.6	14.8	17.8	
	10	41.5	2.9	48.2	1.0	49.1	0.9	23.6	7.2	13.1	15.3	
	15	43.1	2.6	37.7	1.6	50.2	0.4	22.3	8.9	37.9	4.7	
	20	30.7	7.9	47.3	1.0	43.1	2.1	34.2	3.8	28.3	5.8	
Single deprivation	1 ^c	56.4	0.0	20.2	43.4	41.4	7.7	23.5	8.9	54.9	3.6	
Reversal	1	10.7	23.3	8.3	22.9	—	—	9.3	24.0	—	—	
	2	17.7	13.3	11.8	19.7	—	—	11.8	19.7	—	—	
	3	37.1	5.3	26.7	11.1	—	—	26.7	11.1	—	—	
	4	16.7	11.9	25.0	8.8	—	—	25.0	8.8	—	—	
	5	46.2	3.1	24.3	7.9	—	—	24.3	7.9	—	—	
	6	19.5	10.1	21.0	11.1	—	—	21.0	11.1	—	—	
	7	39.5	6.1	40.1	3.3	—	—	40.1	3.3	—	—	
	8	42.1	3.9	50.6	0.6	—	—	50.6	0.6	—	—	
	9	28.8	6.7	35.7	2.3	—	—	35.7	2.3	—	—	
	10	32.5	5.3	53.5	0.9	—	—	53.5	0.9	—	—	
	15	36.1	4.2	55.1	0.5	—	—	37.5	2.3	—	—	
	20	20.4	17.2	41.6	1.5	—	—	35.7	4.2	—	—	
	25	42.9	3.1	51.8	0.3	—	—	31.6	4.9	—	—	
	Single deprivation	1	23.1	7.9	55.2	0.2	—	—	52.7	0.3	—	—
	Single deprivation reversal	1	50.2	5.5	14.4	17.9	—	—	18.3	12.7	—	—
Mean gape amplitude (millimeters)												
Baseline	1	4.8	2.2	9.0	2.6	8.7	1.3	6.0	2.0	11.9	2.0	
	5 ^d	4.3	2.5	9.4	2.7	8.4	0.6	4.6	1.7	13.6	1.8	
	10 ^a	5.1	2.4	10.2	3.0	9.3	1.1	4.2	2.2	13.4	1.8	
	15 ^e	5.5	2.7	10.6	3.1	11.1	1.3	2.9	2.0	14.9	1.2	
	20	3.2	1.9	9.4	2.5	9.3	0.7	5.1	2.4	14.7	2.0	
Single deprivation	1 ^c	5.9	3.1	5.7	1.7	8.2	0.7	2.8	2.0	14.1	1.5	
Reversal	1	3.6	5.9	5.0	9.8	—	—	2.8	5.2	—	—	
	2	3.4	5.3	4.7	8.0	—	—	2.1	3.7	—	—	
	3	4.4	4.8	4.7	7.3	—	—	1.3	1.6	—	—	
	4	2.9	3.5	4.8	5.7	—	—	2.3	2.4	—	—	
	5	4.6	3.7	6.0	7.5	—	—	2.4	2.5	—	—	
	6	3.2	3.0	4.2	3.8	—	—	2.7	2.6	—	—	
	7	5.3	3.6	5.9	4.9	—	—	2.8	2.5	—	—	
	8	5.6	3.4	5.4	4.3	—	—	3.1	2.3	—	—	
	9	4.7	3.2	6.2	3.0	—	—	2.7	2.0	—	—	
	10	5.0	2.8	6.6	3.1	—	—	2.2	1.9	—	—	
	15	6.7	3.7	6.6	3.6	—	—	3.4	2.4	—	—	
	20	4.9	2.5	7.9	3.4	—	—	3.2	1.9	—	—	
	25	6.5	3.6	7.3	3.6	—	—	4.7	3.1	—	—	
	Single deprivation	1	5.0	3.2	8.4	4.7	—	—	4.5	2.9	—	—
	Single deprivation reversal	1	6.4	3.0	4.9	2.4	—	—	1.7	1.5	—	—
Mean key-peck duration (in milliseconds)												
Baseline	1	30	54	35	60	44	77	29	123	24	86	
	5 ^d	39	127	33	66	43	76	30	78	30	75	
	10 ^a	31	151	34	208	52	79	43	123	34	263	
	15 ^e	31	78	32	135	53	148	63	151	19	179	
	20	45	190	34	120	41	131	41	203	23	285	

APPENDIX

(Continued)

Condition	Ses- sion	P1		P2		P3		P4		P5	
		Food	Water	Food	Water	Food	Water	Food	Water	Food	Water
Single deprivation	1 ^c	33	100	38	103	43	57	48	220	22	63
Reversal	1	281	41	101	32	—	—	351	82	—	—
	2	106	39	89	32	—	—	153	66	—	—
	3	71	53	68	30	—	—	119	80	—	—
	4	113	56	69	50	—	—	82	96	—	—
	5	57	66	52	49	—	—	89	120	—	—
	6	80	60	64	58	—	—	79	102	—	—
	7	68	69	39	50	—	—	74	170	—	—
	8	56	86	39	60	—	—	74	178	—	—
	9	69	63	40	74	—	—	71	209	—	—
	10	53	54	41	79	—	—	94	363	—	—
	15	42	66	34	114	—	—	55	240	—	—
	20	61	63	43	560	—	—	37	144	—	—
	25	36	61	36	69	—	—	41	317	—	—
Single deprivation	1	48	60	37	58	—	—	32	54	—	—
Single deprivation reversal	1	29	64	50	193	—	—	66	224	—	—

Note. Data recording failed in the sessions as indicated. However, the correct experimental contingencies were always in effect:

^a Session 9 for 10 for P1.

^b Session 14 for 15 for P2; Session 13 for 15 for P3.

^c Session 3 for 1 for P1 and P2.

^d Session 4 for 5 for P4.

^e Session 14 for 15 for P2; Session 13 for 15 for P3 and P4.