Conjunctive differentiation of gape during food-reinforced keypecking in the pigeon

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The pigeon's keypecking response includes both a head-transport (peck) and a jaw-movement (gape) component. Because the two components are mediated by different effector systems, they may potentially be viewed as orthogonal responses. A response differentiation procedure was used to bring gape amplitude under operant control. The procedure employed a conjunctive response requirement in which reinforcement was contingent upon both gaping and key contact. The key-contact requirement was held constant, while the gape contingency was systematically varied to reinforce either decreases or increases in gape amplitude with respect to baseline. The procedure was effective in shifting the gape distributions in both the upward and downward directions and in inducing new gape values that deviated from the baseline in the reinforced direction. These observations indicate that gape may be brought under operant control. However, subjects showed a bias in the differentiation of the gape response, such that larger gapes were more readily differentiated than smaller gapes. The results are discussed in relation to the methodological utility of the paradigm, the problem of biological constraints on learning, and the heuristic utility of a response components analysis.

The pigeon's keypecking behavior is among the most frequently used response measures in experimental psychology, yet its taxonomic status has been widely debated. Conditioned keypecking was initially viewed as the paradigmatic example of an operant response, but there is now a considerable body of data that supports its classification as a respondent. These include the phenomenon of autoshaping (Brown & Jenkins, 1968; Hearst & Jenkins, 1974), the acquisition of keypecking on omission schedules (Williams & Williams, 1969), and similarities in the topography of conditioned and ingestive pecking responses (Jenkins & Moore, 1973; Wolin, 1968). Other studies, however, have shown that behavior in autoshaping and omission paradigms may be influenced by operant processes (e.g., Allan & Matthews, 1983; Deich & Wasserman, 1977; Jenkins, 1977; Locurto, 1981). The cumulative effect of this research has been to blur the distinction between operants and respondents, and bring into question the utility of that distinction (e.g., Williams, 1981).

One possible reason for the confusion is that research has failed to recognize that conditioned pecking, like ingestive pecking, is not a unitary response but an assemblage of discrete response components, including locomotion, head transport, and gape (LaMon & Zeigler, 1984, 1988; Wasserman, Franklin, & Hearst, 1974; Zeigler, Levitt, & Levine, 1980). The focus of the present study was on the head-transport and gape components. The transport component is mediated by the neck muscles and involves movement of the head toward a target; the gape component is mediated by the jaw muscles and involves opening and closing movements of the beak (LaMon & Zeigler, 1984; Zeigler et al., 1980). The two components are experimentally dissociable, since gape responses may be elicited in head-fixed pigeons in the absence of head transport (Mallin & Delius, 1983). Moreover, the two components have been found to differ in the extent to which their conditioned response topographies resemble their unconditioned response topographies. The gapes of conditioned keypecks resembled those made to food or water reinforcers, whereas the transport component of the conditioned pecking response involved forces that were significantly different from those of unconditioned responses (LaMon & Zeigler, 1988). These

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and other observations (e.g., Klein, Deich, & Zeigler, 1985) suggest that the transport and gape components, although functionally related, may be controlled by different variables. Thus, in considering the taxonomic status of conditioned keypecking, it would be useful to determine the extent to which each of its components are differentially susceptible to influence by operant and/or respondent processes.

Control of the transport component of the conditioned keypeck may involve variations in rate (e.g., Ferster & Skinner, 1957), duration (Zeiler, Davis, & DeCasper, 1980; Ziriax & Silberberg, 1978), force (Chung, 1965; Cole, 1965), and location (Allan & Zeigler, 1987; Eckerman, Hienz, Stern, & Kowlowitz, 1980). All of these pecking-response parameters have been shown to be sensitive to response-reinforcer contingencies during food-reinforced pecking. No comparable studies of the gape component have been carried out.

Gape (i.e., interbeak distance) is an essential topographic feature that differentiates eating from drinking behavior in the pigeon. For eating, the pigeon's jaw movements are episodic, producing gapes whose amplitudes vary with the size of the food object (Deich, Klein, & Zeigler, 1985; Zeigler, et al., 1980); for drinking, the movements are rhythmic, stereotyped in pattern, and made with small and almost invariant gapes (Klein, LaMon, & Zeigler, 1983).

Although there have been no formal studies of the control of gape by either operant or respondent processes, suggestive evidence for respondent control comes from studies of conditioned-pecking-response topography. Differences between the gapes of eating and drinking responses also distinguish conditioned keypecking responses reinforced by food or water (see Jenkins & Moore, 1973, Figure 2). In a quantitative comparison of gape during ingestive and conditioned responses, LaMon and Zeigler (1984, 1988) found that both eating responses and conditioned keypecks for a food US were made with relatively large gapes. Moreover, they found that gapes associated with conditioned keypecks were similar in size to gapes made to the reinforcer. In contrast, both drinking responses and conditioned keypecks for a water US were made with a very small and relatively invariant peak gape. The data on response topography have suggested that autoshaping reflects a Pavlovian process in which control of the unconditioned pecking response is transferred from the food or water reinforcer to the key (Jenkins & Moore, 1973).

Alternatively, it has been proposed that the conditioned pecking response reflects "biologically preorganized appetitive behavior patterns" (Woodruff & Williams, 1976, p. 12). To the extent that this is the case, the gape component of the keypeck response may be subject to biological constraints that might limit either the direction or the extent of the differential reinforcement of gape. For example, if the gape of a food-reinforced keypeck tends to reflect the size of the reinforcer (LaMon & Zeigler, 1984), then this relationship may effectively preclude the differentiation of a wide range of gape sizes when a single pellet size is used as the reinforcer.

These issues were explored using a response differentiation procedure to bring gape under operant control. Gape was monitored continuously and measured directly, using a movement transducer. The differentiation procedure employed a conjunctive response requirement in which reinforcement was contingent upon both gaping and key contact. Thus it involved both the gape and transport components of the keypecking response. Because the two components are mediated by separate anatomical systems, gape amplitude (the differentiated response) is not mechanically constrained by key contact (the conjunctive response), and gape and key contact may therefore be viewed as anatomically orthogonal responses. In addition, because gape amplitude may, in principle, assume any value without affecting the transport component, it is possible to determine a set of baseline values for gape that are unconstrained by reinforcement contingencies. Using this conjunctive differentiation paradigm, the key-contact-response requirement was held constant while the gape contingency was systematically varied to reinforce either increases or decreases in gape amplitude with respect to baseline.

METHOD

Subjects
Three experimentally naive White Carneau pigeons were individually housed and maintained at between 75% and 85% of their free-feeding weights by restriction of their daily food intake.

Apparatus
Testing was carried out in a 31.5×34×35.5 cm operant conditioning chamber with walls and ceiling of clear Plexiglas and a wire-mesh floor. The ceiling was modified for the insertion of a mercury commutator (Scientific Prototype). The front wall, which was painted gray, functioned as an intelligence panel and contained the aperture of a food hopper (9×10 cm) 5.5 cm above the chamber floor and a set of three standard (2.5-cm) pecking-response keys 23.5 cm above the floor. Only the center key was used, and, when activated, it was transilluminated with red light. To decrease the likelihood of damage to the beak-mounted gape transducers (see below) the key was modified with a 6-mm Plexiglas insert that raised its surface to almost level with the chamber wall. The feeder was constructed from a standard watch glass (diameter, 5 cm) mounted at the end of a solenoid-operated lever. During reinforcement, a hopper light was turned on and the solenoid raised the watch glass into a position flush against and concentric with a 5-cm aperture cut into an 18-mm-thick Plexiglas block. A Gerbrands feeder delivered pellets to the watch glass through a 12.7-mm tube inserted into the side of the block. Release of the solenoid lowered the watch glass into a receptacle to dispose of any remaining pellets. The test chamber was located within an acoustically shielded outer chamber illuminated by a 25-W houselight.

"On-line" monitoring of gape. Gape (i.e., interbeak distance) was transduced using a Hall-effect integrated circuit (Panasonic IC No. DN6835), which outputs a voltage monotonically related to the strength of an applied magnetic field. By mounting the Hall-effect device on the upper beak and a samarium-cobalt magnet on the lower beak (Figure 1A) a continuous voltage output was obtained that was proportional to the distance between the two beaks (Figure 1B). The resulting analog voltage was amplified and digi-

A

Key contacts

B
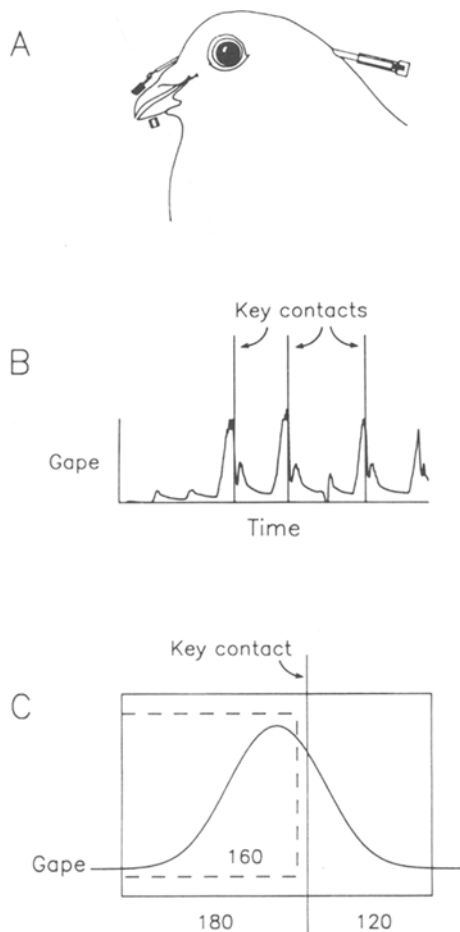
Gape

Time

Key contact

C

Gape ——— 160

180   120

Figure 1. "On-line" monitoring of gape in the pigeon: (A) Diagram of the Hall-effect assembly illustrating the electrode assembly exiting the scalp, the Hall-effect IC on the upper beak, and the samarium-cobalt magnet on the lower beak. (B) Illustrative examples of gape records taken by the Hall-effect system during a keypecking response. (C) Schematic diagram illustrating the acquisition of gape data during keypecking. Variation in gape amplitude and the moment of key contact are indicated. The solid-line box represents the entire envelope of gape data stored and written to disk. A total of 300 msec of gape data were stored—180 msec prior to key contact and 120 msec after contact. The dashed-line box depicts the 160-msec window of gape data that was scanned, in real time, for the peak gape. Reinforcement decisions were made on-line on the basis of this peak value.

tized by an A/D interface. The Hall-effect device was linked to the monitoring system via a connector through the mercury swivel. The transducing system has been described in detail elsewhere (Deich, Houben, Allan, & Zeigler, 1985).

At the start of each test session, the system was calibrated by recording the digital readouts produced first when the jaws were fully closed and then with the jaws opened to varying degrees by the insertion of a graded series of spherical stimuli, 3.2 to 20 mm in diameter. Data acquisition and recording, conversion of analog values into gape size, and control of scheduling were carried out by an Apple IIE microprocessor programmed in the First Language (Scandrett & Gormezano, 1980).

Monitoring of gapes during operant key-pecking. Throughout each trial, the output of the Hall-effect system was continuously

monitored at 250 Hz. At the moment of key closure, the 45 preceding (180 msec) and the 30 succeeding samples (120 msec) of Hall-effect data were stored in a data array. The first 40 points of the array were then scanned, and the highest value was selected and converted to millimeters of gape. Thus, the gape measured for any response was the maximum gape that occurred in a temporal window that extended from 180 msec prior to key closure to 20 msec prior to closure. Preliminary observations had indicated that this interval included virtually all peak gapes during keypecks. To insure that the gape signal was uncontaminated by key contact, the final 20 msec of data were not used to determine peak gape. For each keypeck, all 75 samples used to measure gape were stored to disk. Figure 1C presents a schematic diagram of data acquisition relative to key contact.

Procedure

The study involved three distinct phases carried out in daily sessions of 30 trials (pretraining) or 32 trials (baseline testing, response differentiation). In all phases, reinforcement consisted of the delivery of three 4.9-mm pellets (94 mg; Bioserv, Summit, NJ).

Pretraining. Stable keypecking was established using an autoshaping paradigm (60-sec variable intertrial interval; 8-sec keylight CS) that was modified so that a keypeck during the CS produced an immediate reinforcer. The subjects then underwent several additional days of training on an increasingly lean series of operant schedules (CRF, VI 10 sec, VI 30 sec), designed to engender stable and reasonably high response rates and a resistance to extinction sufficient to carry them through the differentiation phase.

Following the completion of pretraining, the subjects were lightly anesthetized with Equithesin and mounted with the Hall-effect chip and the magnet. The procedure described in Deich, Houben, et al. (1985) was modified so that the IC and magnet were held in place with a cyanoacrylate glue and filler, rather than screws, to reduce damage to the beak. Mounts that came loose were repaired in the same manner. A recovery period of at least 24 h elapsed between mounting and the first experimental session.

Baseline testing. This phase involved a discrete-trial CRF procedure. Trials began with the onset of the keylight, which was terminated by the first keypeck and followed by reinforcer delivery. Trials were separated by a 2-sec intertrial interval. Digitized gape values associated with each keypeck were stored to disk.

Response differentiation. This phase was identical to baseline testing except for the addition of a response differentiation requirement. Reinforcers were delivered only for those keypecking responses whose associated gapes met a predetermined size criterion. Gapes that did not meet the criterion were followed by keylight offset and a 5-sec time-out. The houselight remained on throughout the session.

The procedures for determining the gape criterion at each session were designed to minimize long periods of nonreinforced responding. At the end of each session, a distribution of gape amplitudes for that session was plotted in 1-mm bins. Depending upon the direction of differentiation, the criterion for the next session was set at the 20th percentile (downward) or the 80th percentile (upward) of the gape distribution for the preceding session. The only restriction on changing a criterion was that the change not exceed 3 mm between sessions. Successful differentiation was defined as a shift in all gape parameters (mean, median, mode) combined with the induction of new gape values in the reinforced direction. A given phase (upward or downward) remained in effect until the bird's responding met a stability criterion of three successive sessions with no more than three gape responses in a new bin.

All subjects went through an initial baseline phase, a first differentiation phase, a second baseline phase, a second differentiation phase, and a final baseline phase. Two of the subjects (84-89, 85-28) were reinforced for making keypecks with progressively smaller gapes in the first differentiation phase and progressively larger gapes in

Table 1
Training History of Each Subject

Subject	Phase	Session (Type)	RF Density	SD	Range
84-89	B	1			
	D1	19(D)	30.5	20.8	5.3-100
	B	7			
	D1	7(U)	62.5	24.7	34-100
	B	1			
85-01	B	1			
	D1	5(U)	71	19.2	40-91.4
	B	5			
	D2	7(D)	62.5	24.7	34-100
	B	1			
85-28	B	1			
	D1	7(D)	31.8	15.4	15.8-65.3
	B	4			
	D2	16(U)	40.3	25.6	9.6-80
	B	7			

Note—B = baseline sessions, D1 = first differentiation phase, D2 = second differentiation phase; Sessions (Type) = number of sessions and type (U = upward; D = downward); RF Density = mean percentage of session trials ending in reinforcement; SD = standard deviation of RF density (%); Range = lowest and highest RF density values (%).

the second differentiation phase. This arrangement was reversed for the third subject (85-01). Table 1 summarizes the training history of each subject.

RESULTS

Figure 2 illustrates the time course of changes in mean gape for each of the subjects across the different phases of the experiment. At the start of training, all birds keypecked with gape values considerably greater than 0 mm. For all of the subjects, imposition of the response differentiation procedure produced a shift away from baseline values in a direction appropriate to the imposed gape-size requirement. For Bird 85-01, reinforcers were first delivered for gapes greater than baseline, and the emitted gapes increased over successive sessions. Removal of the gape criterion was followed by a decrease in emitted gapes toward baseline levels. Imposition of a criterion gape smaller than baseline was followed by a gradual decrease in mean emitted gape. Comparable control by the contingency was seen in Bird 85-28, in which the differentiation requirements were imposed in the reverse order. For Bird 84-89, the effects of the contingency were more variable, but the general trends were similar.

For 2 of the birds (84-89, 85-01), differentiation was more rapid in the direction of larger gapes; the relationship was reversed for Bird 85-28. The performance of 2 of the birds (84-89, downward phase; 85-28, upward phase) showed sudden rebounds toward baseline levels and then a gradual return toward the differentiated direction. For all subjects, mean gape values for the terminal session of upward differentiation were further removed from baseline values than were those for the terminal session of downward differentiation.

Figure 3 presents frequency distributions of gape sizes for the initial baseline testing session of each bird and for the final session under each of the response differentiation conditions. The data indicate (1) that differential reinforcement produced a marked shift in the distribution of gape sizes, (2) that, in all cases, this shift was in the direction of the criterion requirement, and (3) that it also involved the induction of gape sizes not seen during the baseline condition. It should be noted, however, that although very large gapes (>15 mm) were quite frequent in the "larger than" condition, very small gapes (<4 mm) were infrequent, even when the "smaller than" criterion was in force.

For each subject, the data relating required to emitted gape were plotted separately for the upward and downward differentiation phases (Figure 4A). A regression analysis was performed on the mean gape data, with daily criterion and direction of differentiation as predictors. Also, effects that involved subjects and interactions with subjects were calculated. Only one effect involving subjects was significant. The criterion effect differed significantly between subjects [$F(2,61) = 3.37$, $p < .05$]. The graphs of the individual subject data provided no clear interpretation for this effect. The significant main effect of direction [$F(1,61) = 10.488, p < .05$] confirmed that gape was larger overall in the upward condition than in the downward condition. The overall positive linear relationship between the criterion and
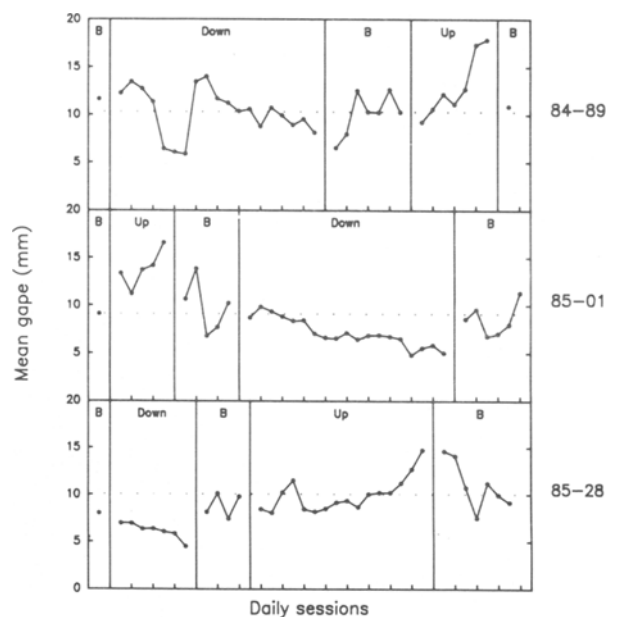

Figure 2. Session means for gapes recorded across all the experimental phases for each of the subjects. Phases are separated by solid vertical lines and are designated as Up, Down, and B (baseline). Horizontal dotted lines represent the grand mean of all baseline sessions for each subject.
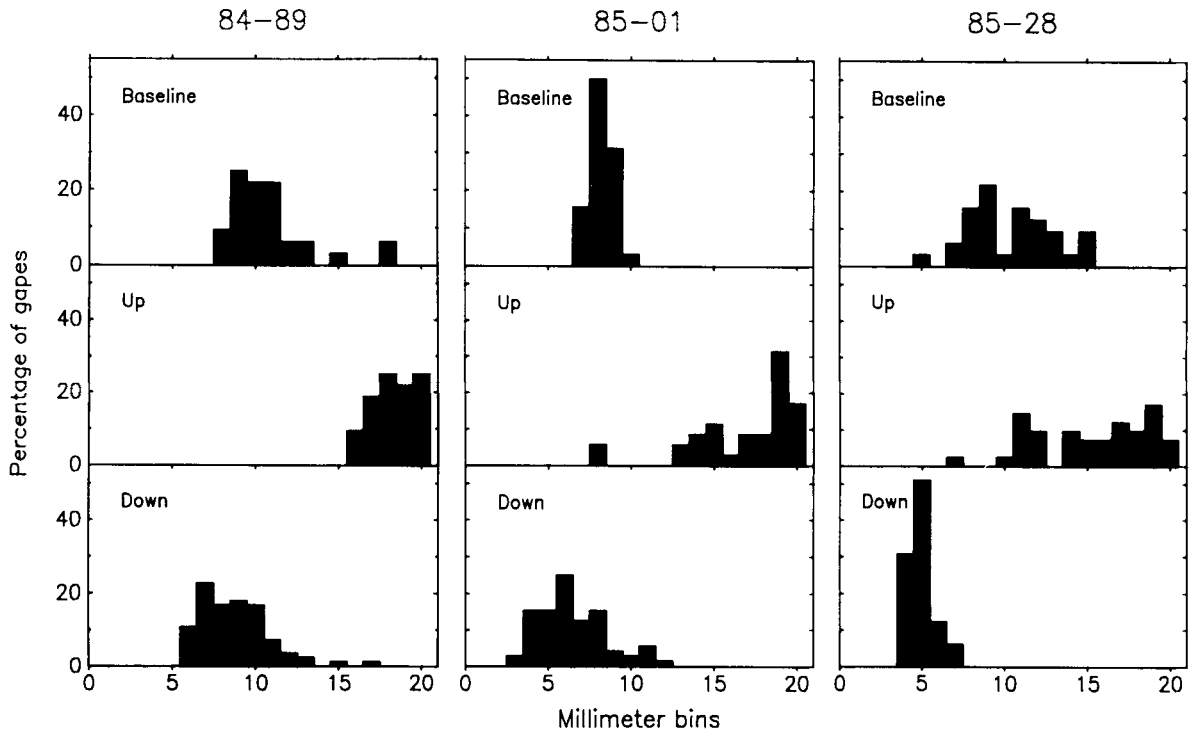
Figure 3. Frequency distributions of gapes (1-mm bins) during the initial baseline condition and the final session under each of the response differentiation conditions.

mean gape was confirmed by a significant correlation of the two $[F(1,61) = 40.26, p < .001]$. Finally, a significant interaction of direction and criterion $[F(1,61) = 6.635, p < .05]$ confirmed that the slopes of the best-fitting lines were greater in the upward condition than in the downward condition. The overall r^2 for this regression model was 0.814.

While the data plotted in Figure 4A indicate that gape amplitude is a function of criterion gape, they also suggest a bias toward the emission of larger gapes. The dotted diagonal line indicates values at which criterion and mean gape are equal. Optimal gape values would be slightly above this line for upward differentiation and slightly below it for downward differentiation. However, during downward differentiation, data points are typically above the dotted line; that is, a gape equal to the mean gape would not have been reinforced. In the upward differentiation phase, mean gape tends not only to exceed criterion values, but to do so by a considerable amount. A gape criterion of only 12-13 mm was adequate to induce mean gapes that were substantially larger. Examination of the data on mean reinforcement density for each phase (Table 1) supports these observations. For all subjects, higher densities of reinforcement were consistently seen during the upward differentiation phase, suggesting that the upward contingency exerted stronger differential control (see Table 1). However, the variability in reinforcer density observed in both upward and downward phases (see range values in Table 1), suggests that the recorded gape-amplitude changes were not due to reinforcer density changes alone.
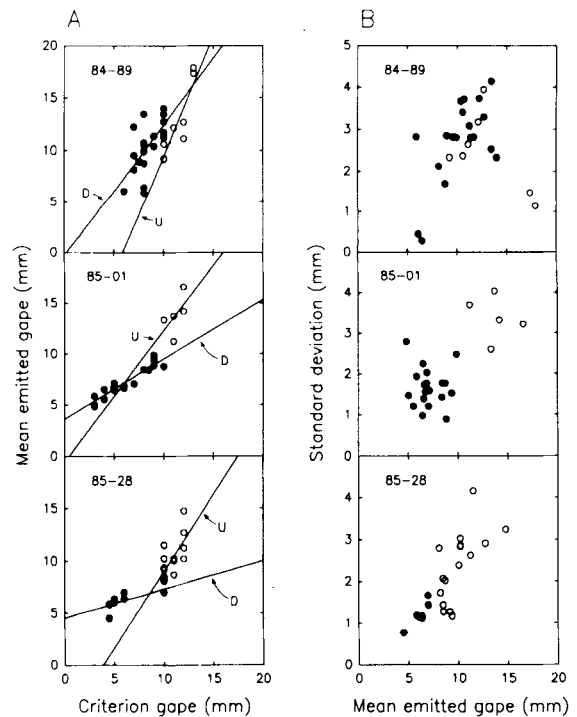

Figure 4. (A) Scatterplots of mean emitted gape as a function of criterion gape for each subject, for all differentiation phases. Filled circles represent downward differentiation; open circles represent upward differentiation. Dotted lines represent matching of emitted gape to criterion gape. Solid lines represent separate regression functions upward (U) and downward (D) differentiation, as indicated. (B) Relation between mean emitted gape and its standard deviation for each of the birds across all differentiation sessions.

Figure 4B plots standard deviations for emitted gape as a function of mean gape. For 2 of the subjects (85-01, 85-28) there was a positive, monotonic relationship between mean gape and its accompanying standard deviation. For 84-49, standard deviation increased with mean gape up to about 12 mm and decreased thereafter.

DISCUSSION

This study demonstrated that the amplitude of the pigeon's gape response may be brought under operant control by appropriate manipulation of response-reinforcer contingencies. The mean, median, and mode of the gape distribution were shifted in both the upward and the downward directions, and, in all cases, the procedure resulted in the induction of new gape values, which deviated from baseline in the predicted direction. The relationship between required and emitted gape is best described by linear functions, and in this respect it is similar to a number of psychophysical relationships, including pecking-response duration and interresponse time (temporal differentiation schedules), both of which are power functions of the criterion value (see, e.g., Platt, 1979; Zeiler, 1979; Zeiler et al., 1980). Finally, the results suggest a bias in the differentiation of the gape response such that larger gapes are more readily differentiated than smaller gapes.

The near-linear relationship between mean gape and the within-subject standard deviation of gape agrees with that found by Schmidt (1980, 1982) for the force and duration of human hand movements. In those studies, the same increasing relationship was found between mean produced force, mean movement time, and their associated within-subject standard deviations. The increase in standard deviation in these motor systems with increasing magnitude of movement parallels the increase in the just noticeable difference (jnd; expressed in physical stimulus units) with increases in stimulus intensity. These relationships are well represented by Weber's law. Similar findings have been reported for the relationships between mean interresponse time (Platt, 1979; Zeiler, 1979), reinforced peck durations (Zeiler et al., 1980), and interval length estimation (Gibbon, 1977), on the one hand, and their associated measures of standard deviation, on the other. The similarity of outcomes for sensation and motor production may suggest common or similar neural mechanisms. One possibility is that motor behavior is partially governed by sensory or neural timing mechanisms that are themselves subject to Weber's law.

The present experiment has minimized some of the methodological factors which are potentially capable of confounding response differentiation studies. In many previous studies, only increases in the response parameter under study have been reinforced (e.g., Chung, 1965; Platt, 1979; Zeiler et al., 1980). This may be because, even in the absence of any differential response requirement, some value along the response continuum is required to complete the operant. Barpressing and keypecking, for example, always require some force or duration, and rate of responding cannot be reduced to zero without

eliminating the operant itself. This methodological constraint is absent in the present study. Since the differentiated response (gape) is free to vary in any direction while the conjunctive response (key contact) is held constant, the conjunctive differentiation paradigm makes possible the determination of an unconstrained baseline value as well as the reinforcement of both increases and decreases in gape with respect to that baseline. Because the differentation of gape is bidirectional, it is unlikely that our results reflect any unconditioned relationship between gape size and reinforcer density (see Table 1), analogous to the increases in force that have been reported during extinction (Skinner, 1938).

The present study involves direct, rather than manipulandum-based, measurement of the differentiated response (gape). Manipulandum-based differentiation studies may leave unspecified the response parameter that is actually differentiated. It is possible, for example, that what appears to be the successful differentiation of a specific response parameter is achieved by adventitious, but selective, reinforcement of alternative response topographies that may satisfy the required contingency. Thus, apparent differential reinforcement of leverpressing durations could actually reflect not the differentiation of a duration parameter, but the differential reinforcement of topographically different responses requiring greater lengths of time to complete. Similarly, in experiments on peck duration, increases in peck force could result in increasing key displacements that are interpreted as increases in pecking-response duration (LaMon, 1981). To the extent that the transport and gape components of the pigeon's pecking response are anatomically orthogonal, these possibilities are minimized. Our observations of subjects in the present experiment suggest that variations in the topography of the transport component do not affect gape in any systematic manner (see also LaMon & Zeigler, 1988). Indeed, Mallin and Delius (1983) have demonstrated operant control of gape frequency in head-fixed pigeons, where a transport component is presumably lacking.

The present data are also relevant to the issue of biological constraints on learning. Such constraints are presumed to follow from the fact that the pigeon's pecking response, rather than being an "arbitrary" motor act, reflects its phyletic history and ecological function. Bringing pecking under operant control may not remove those constraints. Instead, the topography of keypecking (i.e., its force, rate, duration, or gape) may continue to reflect the species-typical characteristics of the ingestive pecking (e.g., Staddon, 1977; Timberlake & Lucas, 1985). Such topographic constraints could be manifested either as a bias toward particular values of a specific response parameter or as a limitation in the extent or direction of its differentiation.

Evidence for such constraints has been noted in response differentiation experiments designed to bring pecking-response parameters under operant control. Both peck duration (Zeiler et al., 1980) and interresponse time (Kramer & Rilling, 1965) appear to be sensitive to operant contin-

gencies only over a limited portion of their possible ranges. These observations may be interpreted as indicating that operant control of peck duration and rate for a food-reinforced response is limited to changes occurring within a range of durations or rates characteristic of the pigeon's eating response (see, e.g, Lejeune & Richelle, 1982).

In the present experiment, several observations suggest the operation of some types of constraints or biases in the differentiation of gape. There was, first, a bias toward baseline values, evident in a tendency to return to that value at the end of each differentiation phase (i.e., after the removal of the differential contingency). This was an unexpected finding, since, in the absence of a specific contingency, the existing gape values will continue to be reinforced. Furthermore, all subjects showed a bias toward the induction of large gapes and a resistance to the induction of gapes below baseline values. Since none of these findings are readily explicable in terms of reinforcement operations, they may reflect other sources of control.

The bias towards larger gapes may result from functional considerations related to the grasping task. Pecks made with gapes smaller than the diameter of the target seed will almost always be unsuccessful because they will deflect the seed to the side (Levine & Zeigler, 1981). Gapes that are substantially larger than target size have no adverse consequences. This asymmetry in task demands may be related (ontogenetically or phylogenetically) to the observed asymmetry in gape differentiation.

The bias toward baseline values of gape could reflect "natural" limits below which that parameter cannot be manipulated (DeCasper & Zeiler, 1977). For gape, the "natural" upper and lower limits may be set—in an absolute sense—by the morphology of the jaw, with closed beaks at one extreme and fully open beaks at the other. Within this "natural" range, additional (relative) limits may be set by deprivation state and/or reinforcer properties. In the present study, both possibilities are available. Subjects were food-deprived and food-reinforced. Under these conditions, operant control of gape may be limited to the portion of the gape-size range that lies outside the range of drinking pecks (1–3 mm). The second possibility involves a previous observation that there is a relationship between the size of the reinforcer and the amplitude of gapes associated with food-reinforced keypecks (LaMon & Zeigler, 1984). In the present study, the fact that a 4.9-mm pellet served as the reinforcer may have precluded the differentiation of smaller gape sizes. The first hypothesis could be tested by using a water-reinforced keypecking response; the second could be tested by using smaller pellet sizes as reinforcers.

The demonstration that the gape response is sensitive to its consequences supports the contention that gaping (e.g., gapes occurring during the grasping phase of feeding) in the pigeon approximates the functional complexity of prehensile behavior in primates (Klein et al., 1985). In contrast to human grasping, control of gape in the

pigeon is mediated by a relatively simple effector system (the jaw) comprising only seven muscles and involving movement about a single joint (Klein et al., 1985). It may thus be a useful model system for studies of neural mechanisms (Bermejo, Houben, Allan, Deich, & Zeigler, 1987; Wild, Arends, & Zeigler, 1985).

CONCLUSIONS

The present study of gape differentiation has several features of methodological interest. First, the conditioning paradigm (conjunctive differentiation) employed a response requirement in which reinforcement was contingent upon the performance of two anatomically orthogonal responses, gape and key contact, involving different components of the pigeon's pecking response. Second, the experimental procedure involved a direct, rather than a manipulandum-based, measure of the differentiated response.

The convention of manipulandum-based measurement may have its theoretical roots in Skinner's emphasis on the environmental effects of a response and its empirical origin in the difficulties involved in the measurement of an anatomically defined response system on a time base that permits rapid decisions as to reinforcer delivery. However, if our interest is in the susceptibility of individual response components to operant or respondent control, the direct measurement and differentiation of anatomically defined response components is essential. Moreover, in addition to its utility in the present context, the conjunctive differentiation paradigm may provide a useful tool for the study of the coordination of two anatomically defined responses. The simultaneous measurement of two responses with joint contingencies seems to be the minimal condition for examining the role of reinforcement in coordinating complex, multicomponent responses.

The present results are also of theoretical interest, since they indicate that gape amplitude may be brought under operant control during food-reinforced keypecking. Using operant procedures and a water reinforcer, Mallin and Delius (1983) have previously demonstrated differentiation of gape frequency in the head-fixed pigeon. Studies of gape during autoshaping (Jenkins & Moore, 1973; LaMon & Zeigler, 1984, 1988) have provided suggestive (though not definitive) evidence for its respondent control. Thus, the gape component of the pigeon's conditioned keypecking behavior appears to be a biconditional response (Williams, 1981), amenable to control by both respondent and operant contingencies. A similar conclusion has been reached with respect to several parameters of the transport component, including duration (Schwartz & Williams, 1972; Ziriax & Silberberg, 1978), location (Allan & Zeigler, 1987; Eckerman et al., 1980), and rate (Allan & Matthews, 1983; Ferster & Skinner, 1957).

Finally, these results suggest that it may be heuristically useful to view conditioned keypecking as a set of discrete response components mediated by different ef-

fector systems. Each component may potentially contribute to the observed result of an experimental manipulation. For example, in studies of interresponse time (IRT), long IRTs often involve locomotion away from the key, short IRTs have been shown to result from separate counts of key contact by the top and bottom beaks (Smith, 1974), and other IRTs may reflect only variations in the head transport component. Since conditioned pecking is generally defined by its effects upon a manipulandum (response key), the contribution of individual components tends to be neglected. Instead, attention is focused upon the pecking response as a whole, rather than upon the control of its individual components by operant and/or respondent processes. Consequently, because pecking-response components (1) may be controlled by different sets of variables, and (2) may be differentially susceptible to operant and respondent processes, a unitary distinction between the operant and respondent control of keypecking may not be sustainable.

REFERENCES

ALLAN, R. W., & MATTHEWS, T. J. (1983, April). *The omission of autoshaped keypecks in a delay of reinforcement procedure.* Paper presented at the 54th Annual Meeting of the Eastern Psychological Association, Baltimore.

ALLAN, R. W., & ZEIGLER, H. P. (1987). The control of response location. *Eastern Psychological Association Abstracts,* **178**, 24.

BERMEJO, R., HOUBEN, D., ALLAN, R. W., DEICH, J. D., & ZEIGLER, H. P. (1988). *Prehension in the pigeon: I. Descriptive analysis.* Manuscript submitted for publication.

BROWN, P. L., & JENKINS, H. M. (1968). Autoshaping of the pigeon's keypeck. *Journal of the Experimental Analysis of Behavior,* **11**, 1-8.

CHUNG, S. (1965). Effects of effort on response rate. *Journal of the Experimental Analysis of Behavior,* **8**, 1-7.

COLE, J. L. (1965). Force gradients in stimulus generalization. *Journal of the Experimental Analysis of Behavior,* **8**, 231-241.

DeCASPER, A. J., & ZEILER, M. D. (1977). Time limits for completing fixed ratios: IV. Components of the ratio. *Journal of the Experimental Analysis of Behavior,* **27**, 235-244.

DEICH, J. D., HOUBEN, D., ALLAN, R. W., & ZEIGLER, H. P. (1985). "On-line" monitoring of jaw movements in the pigeon. *Physiology & Behavior,* **35**, 307-311.

DEICH, J. D., KLEIN, B. G., & ZEIGLER, H. P. (1985). Grasping in the pigeon: Mechanisms of motor control. *Brain Research,* **337**, 362-367.

DEICH, J. D., & WASSERMAN, E. A. (1977). Rate and temporal pattern of key pecking under autoshaping and omission schedules of reinforcement. *Journal of the Experimental Analysis of Behavior,* **27**, 399-405.

ECKERMAN, D. A., HIENZ, R. D., STERN, S., & KOWLOWITZ, V. (1980). Shaping the location of the pigeon's peck: Effect of rate and size of shaping steps. *Journal of the Experimental Analysis of Behavior,* **33**, 299-310.

FERSTER, C. B., & SKINNER, B. F. (1957). *Schedules of reinforcement.* New York: Appleton-Century-Crofts.

GIBBON, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological Review,* **84**, 279-325.

HEARST, E., & JENKINS, H. M. (1974). *Sign tracking: The stimulus-reinforcer relation and directed action.* Austin, TX: Psychonomic Society.

JENKINS, H. M. (1977). Sensitivity of different response systems to stimulus-reinforcer and response-reinforcer relations. In H. Davis & H. M. B. Hurwitz (Eds.), *Operant-Pavlovian interactions* (pp. 47-66). Hillsdale, NJ: Erlbaum.

JENKINS, H. M., & MOORE, B. R. (1973). The form of the autoshaped response with food or water reinforcers. *Journal of the Experimental Analysis of Behavior,* **20**, 163-181.

KLEIN, B. G., DEICH, J. D., & ZEIGLER, H. P. (1985). Grasping in the pigeon (*Columba livia*): Final common path mechanisms. *Behavioral Brain Research,* **18**, 201-213.

KLEIN, B. G., LAMON, B. C., & ZEIGLER, H. P. (1983). Drinking in the pigeon (*Columba livia*): Topography and spatiotemporal organization. *Journal of Comparative Psychology,* **97**, 178-181.

KRAMER, T. J., & RILLING, M. (1970). Differential reinforcement of low rates: A selective critique. *Journal of the Experimental Analysis of Behavior,* **8**, 19-28.

LAMON, B. C. (1981). *Conditioned and consumatory grasping in the pigeon.* Unpublished doctoral dissertation, Hunter College, City University of New York, New York.

LAMON, B. C., & ZEIGLER, H. P. (1984). Grasping in the pigeon (*Columba livia*): Stimulus control during conditioned and consummatory responses. *Animal Learning & Behavior,* **12**, 223-231.

LAMON, B. C., & ZEIGLER, H. P. (1988). Control of pecking response form in the pigeon: Topography of ingestive behaviors and conditioned keypecks with food and water reinforcers. *Animal Learning & Behavior,* **16**, 256-267.

LeJEUNE, H., & RICHELLE, M. (1982). Differential reinforcement of perching in the pigeon: A comparison with differential-reinforcement-of-low-rate-key-pecking. *Behaviour Analysis Letters,* **2**, 49-57.

LEVINE, R. R., & ZEIGLER, H. P. (1981). Extratelencephalic pathways and feeding behavior in the pigeon. *Brain, Behavior & Evolution,* **19**, 56-92.

LOCURTO, C. M. (1981). Contributions of autoshaping to the partitioning of conditioned behavior. In C. M. Locurto, H. S. Terrace, J. Gibbon (Eds.), *Autoshaping and conditioning theory* (pp. 101-135). New York: Academic Press.

MALLIN, H. D., & DELIUS, J. D. (1983). Inter- and intraocular transfer of color discriminations with mandibulation as an operant in the head-fixed pigeon. *Behaviour Analysis Letters,* **3**, 297-309.

PLATT, J. R. (1979). Inter-response-time shaping by variable-interval-like inter-response-time reinforcement contingencies. *Journal of Experimental Analysis of Behavior,* **31**, 3-14.

SCANDRETT, J., & GORMEZANO, I. (1980). Microprocessor control and A/D acquisition in classical conditioning. *Behavioral Research & Methods Instrumentation,* **12**, 120-125.

SCHMIDT, R. A. (1980). On the theoretical status of time in motor program representations. In G. E. Stelmach & J. Requin (Eds.), *Tutorials in motor behavior* (pp. 145-166). New York: North-Holland.

SCHMIDT, R. A. (1982). Generalized motor programs and schemas for movement. In J. A. S. Kelso (Ed.), *Human motor behavior: An introduction* (pp. 189-238). Hillsdale, NJ: Erlbaum.

SCHWARTZ, B., & WILLIAMS, D. (1972). Two different kinds of key pecks in the pigeon. *Journal of the Experimental Analysis of Behavior,* **18**, 201-216.

SKINNER, B. F. (1938). *The behavior of organisms.* New York: Appleton-Century-Crofts.

SMITH, R. F. (1974). Topography of the food-reinforced key peck and the source of 30-millisecond inter-response times. *Journal of the Experimental Analysis of Behavior,* **24**, 544-551.

STADDON, J. E. R. (1977). Schedule-induced behavior. In W. K. Honig & J. E. R. Staddon (Eds.), *Handbook of operant behavior* (pp. 125-152). Englewood Cliffs, NJ: Prentice-Hall.

TIMBERLAKE, W., & LUCAS, G. (1985). The basis of superstitious behavior: Chance contingency, stimulus substitution, or appetitive behavior. *Journal of the Experimental Analysis of Behavior,* **44**, 279-299.

WASSERMAN, E. A., FRANKLIN, S. R., & HEARST, E. (1974). Pavlovian appetitive contingencies and approach versus withdrawal to conditioned stimuli in pigeons. *Journal of Comparative & Physiological Psychology,* **86**, 616-627.

WILD, J. M., ARENDS, J. J. A., & ZEIGLER, H. P. (1985). Telencephalic connections of the trigeminal system in the pigeon (*Columba livia*): A trigeminal sensorimotor circuit. *Journal of Comparative Neurology,* **234**, 441-464.

WILLIAMS, D. R. (1981). Biconditional behavior: Conditioning without constraint. In C. M. Locurto, H. S. Terrace, & J. Gibbon (Eds.), *Autoshaping and conditioning theory* (pp. 55-99). New York: Academic Press.

WILLIAMS, D. R., & WILLIAMS, H. (1969). Automaintenance in the

pigeon: Sustained pecking despite contingent nonreinforcement. *Journal of the Experimental Analysis of Behavior*, **12**, 511-520.

WOLIN, B. (1968). Differences in manner of pecking a key between pigeons reinforced with food and water. In A. C. Catania (Ed.), *Contemporary research in operant behavior* (p. 286). Glenview, IL: Scott, Foresman.

WOODRUFF, G., & WILLIAMS, D. R. (1976). The associative relation underlying autoshaping in the pigeon. *Journal of the Experimental Analysis of Behavior*, **26**, 1-13.

ZEIGLER, H. P., LEVITT, P., & LEVINE, R. R. (1980). Eating in the pigeon (*Columba livia*): Movement patterns, stereotypy and stimulus control. *Journal of Comparative & Physiological Psychology*, **94**, 783-794.

ZEILER, M. D. (1979). Output dynamics. In M. D. Zeiler & P. Harzem (Eds.), *Reinforcement and the organization of behavior* (pp. 79-115). New York: Wiley.

ZEILER, M. D., DAVIS, E. R., & DeCASPER, A. J. (1980). Psychophysics of key-peck duration in the pigeon. *Journal of the Experimental Analysis of Behavior*, **34**, 23-33.

ZIRIAX, J. M., & SILBERBERG, A. (1978). Discrimination and emission of different key-peck durations in the pigeon. *Journal of Experimental Psychology*, **4**, 1-21.