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THE CONTROL OF RESPONSE FORM: FEEDING AND CONDITIONED RESPONDING IN THE PIGEON

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THE CONTROL OF RESPONSE FORM:
FEEDING AND CONDITIONED RESPONDING IN THE PIGEON

by

Brent LaMon

A dissertation submitted to the Graduate Faculty
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Abstract

THE CONTROL OF RESPONSE FORM:
FEEDING AND CONDITIONED RESPONDING IN THE PIGEON

by

Brent LaMon

Adviser: Professor H. Philip Zeigler

The control of response form was examined by providing a quantitative analysis of the movements subserving feeding and conditioned responding for food reinforcers. The aim of these experiments was to clarify the stimulus control and sensorimotor organization of these motor patterns. The experimental approach involved specifying a series of common behavioral elements that would characterize both feeding and conditioned keypecking. Based on high-speed cine analysis of the movements, the moment of substrate contact was chosen as an unambiguous temporal landmark that would provide behavioral endpoints for three response elements: beak opening, eye closure and the spatial location (trajectory) of the peck. A photographic system activated at the moment of substrate-contact provided size-calibrated photographs from which measurements of these features of response form were obtained. In order to compare the behaviors under similar testing situations, both feeding and conditioned pecks were directed to a floor-mounted response-key. The response-key incorporated a force transducer so that the peak force and duration of substrate contact was measured for each response.

In the feeding situation a range of seed sizes were placed on the response-key for each bird to eat. For conditioned responses, the following independent variables were examined: (1) contingency-discriminated operant (CRF, VR3, and extinction reinforcement schedules), Pavlovian (autoshaping procedure); (2) reinforcer type- grain (2 seed sizes); ( ) signal properties-targets on signals (black dots of 5 sizes projected on white background), signals as targets (white dots of 5 sizes projected on black background); seed key (seed glued to center of response key).

The major findings of this study can be summarized as follows:

(1) Quantitative descriptions of the form of feeding and conditioned keypeck were provided. Comparison of the form of feeding and conditioned responses showed that the average force of conditioned keypecks is substantially greater than the average force of consummatory pecks. Group means for duration, beak opening and eye closure did not differ statistically.

(2) The autoshaping and operant conditioning procedures produced keypecks of similar form (no statistical differences between groups).

(3) There were no consistent group differences in response

form between the operant CRF and VR3 reinforcement schedules. The extinction schedule produced a slight, but statistically significant, increase in mean peck force.

(4) For nearly all conditioned keypecks the measurements of force and duration were positively correlated, indicating that keypeck duration was primarily determined by the force of impact and the physical properties of the response-key.

(5) For both conditioning groups, shifting to a larger seed size as the reinforcer produced an increase in beak opening that was proportional to the change in the size of the reinforcer.

(6) In the feeding situation, beak opening at the moment of contact was typically greater than seed size. However, the finding that errors (gape smaller than seed size) followed an increase in seed size suggested that beak opening was determined by the size of seeds previously eaten rather than visual information available before each peck is initiated.

(7) Neither black nor white targets on conditioning signals consistently controlled peck location, although the white dots received a significantly greater number of pecks on target for both groups. The operant group showed slight relationship between beak opening and target size with the white-dot stimuli.

(8) In the seed-key condition both conditioning groups initially directed keypecks at the seed, but within the first ten responses the birds stopped treating the seed as a target, pecking around the seed on the periphery of the key. This

sort of outcome-contingent control indicates that continued orientation of peck location requires response-produced proximate sensory feedback provided by a seed in the mouth, while the propensity to peck can be maintained by delayed feedback produced by subsequent access to grain.

These findings suggest that assumptions of a unitary organization for both feeding and conditioned responses (eg. the learned-release of a common fixed action pattern or elicitation of an unconditioned feeding response) provide little explanatory utility in the analysis of response form. The movement patterns examined in this study were composed of several behavioral elements, each with potentially different and independent sources of control. As a detailed analysis of response form, these data provide implications for both behavior theory and neurobehavioral studies of motor-control mechanisms.

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Introduction

Causal Analysis and Behavior

In the study of behavior two principal issues for analysis can be distinguished. The first concerns how different classes of behaviors are distributed in time and the second concerns the form of the movement patterns composing a particular behavior. In both cases an attempt is made to explain behavior in terms of an interaction between the external stimulus environment and the internal state of the organism; what differs is the time scale and units of behavior upon which the analysis is based (Rachlin, 1976; Hinde, 1970). Perhaps because similar causal factors were often assumed to control both the occurence and form of behavior, behavioral research has tended to concentrate on the question of what variables dispose an organism to engage in one class of behavior rather than another, and pass over the question of what factors modulate the form of ongoing behavior. Because it is convenient to identify gross classes of behavior (e.g. feeding, aggression) with respect to function, this has led many studies to deal with such behavior patterns as unitary with respect to causation (e.g. fixed action patterns). But relatively few behaviors have been studied that may be considered the output of a central neural organization and independent of control by stimulus factors once initiated (cf. Bentley and Hoy, 1972). It may be more advantageous to approach the analysis of response form by conceptualizing behavior patterns as organized sequences of effector movements that constitute a motor act.

Considered in this way, motor patterns may be viewed as a series of behavioral elements, each with potentially different sources of control, and each with different degrees of variability depending on the particular behavioral context.

Such an approach is consistent with neuroanatomical evidence which suggests that discrete sensorimotor 'sub-systems' control the spatiotemporal organization of movement in different effector systems. The coordination of muscular contractions among several effector systems to produce a complex skeletal motor pattern is therefore likely to reflect several sources of control. As Hinde (1970) has pointed out, any movement involves a number of muscles contracting in particular relationships with each other and the analysis of a movement sequence should include three possible sources of control: environmental stimuli, proprioceptive stimuli and coordinating mechanisms within the central nervous system. Thus, when several behavioral elements representing different effector systems are combined to produce a behavioral act, analysis of the variables that initiate that behavior does not obviate the need to study the factors controlling its form.

Many behaviors may therefore be considered the output of a response system composed of several behavioral elements, each with potentially different sources of control. Because multiple causal factors are typically operative in the production of a motor pattern, they may be said to provide the behavioral context that determines a particular response. This implies that the analysis of a behavior should proceed by examining the spatiotemporal organization of the movement patterns of interest so that the relevant behavioral elements may be specified. For each element a set of putative controlling variables may then be identified and manipulated so that behavioral outcomes may be related to control by specific features of the response system. The primary aim of this dissertation is to apply such an analysis to the pecking response system of the pigeon in order to examine the control of response form in feeding and conditioning situations.

Pigeon feeding behavior and conditioned keypecking

Feeding. Zeigler, (1976) has provided an extensive review of the pigeon's feeding behavior and suggested several features that make the pigeon an excellent subject for behavioral study. The pigeon's feeding behavior is relatively stereotyped and species-typical; but as a "dietary generalist" the pigeon's eating response is not overly specialized for a single food source and involves stimulus control by both visual and somatosensory information. Normal feeding behavior consists of a quantal response (pecking) that is easily identified and 'digitized' for recording purposes. Furthermore, the movement patterns involved in eating and drinking are distinctive (cf. Zeigler et.al. 1980; Klein and LaMon, 1981) and these differences appear to carry over to conditioned responses maintained by food and water reinforcers (Wolin, 1968;

Jenkins and Moore, 1976). In addition, the work of Karten and co-workers (Karten, 1969; Karten and Hodos, 1967; Cohen and Karten, 1974) on central neural structures taken together with Zeigler's studies of peripheral oro-sensory mechanisms (reviewed in Zeigler, 1976, 1980), has provided an excellent anatomical foundation and basis for continued study of the neurobehavioral mechanisms mediating feeding.

A detailed description of the movement pattern mediating eating in the pigeon has appeared in Zeigler et. al. (1980) and figure 1 summarizes the spatiotemporal organization of these movements. Several features of this response should be noted. First, the approach to food involves a rapid descent of the head toward the substrate during which the eye closes and the beak opens. Contact with the substrate is always quite brief, as the head is immediately withdrawn whether or not a seed is grasped in the mandibles. As the head moves upward, a seed grasped between the beak tips is transferred to the back of the oral cavity with the aid of the tongue and a decelerating movement of the head. The closure of the eye during the downward movement to the seed suggests that the peck is ballistic in nature and does not require visual feedback for guidance once initiated. After the seed is grasped, tactile somatosensory information from the mouth coordinates the subsequent mandibulation and swallowing elements of the response sequence. Studies of trigeminal deafferentation (Zeigler 1975 a&b; Zeigler, Miller and Levine, 1975) indicate that the loss of somatosensory information from the beak and mouth causes a severe disruption of feeding behavior involving both sensory-motor impairment of eating efficiency and 'motivational' impairments reflected by a loss of responsiveness to food and failure to initiate feeding responses.

Conditioned keypecking. Several authors have provided observations from conditioning situations (operant and Pavlovian) that keypecks maintained by food or water reinforcers resemble the form of eating or drinking responses, respectively. The first study to point out the similarity between conditioned keypecks and the consummatory pattern appropriate to the reinforcer was that of Wolin (1948) which examined the responses of pigeons in an operant conditioning situation. Food-reinforced keypecks were observed to be "rapid, short, powerful thrusts of the head with the beak open," while water-reinforced pecks were characterized by "a slow, long, easy pushing motion with the beak almost closed." Despite a rather crude technique for timing responses, the duration of food-reinforced pecks was found to be substantially shorter than keypecks for water reinforcement. It is interesting to note that this was one of the first reports that suggested that features of the conditioning situation other than the contingency between response and reinforcement (cf. Skinner, 1938) were affecting certain properties of the response. While many studies went on to demonstrate that explicit response-reinforcer contingencies could exert powerful control over both the distribution and form of responding (e.g. Herrick, 1964; Mintz, 1962; Anger, 1956), it was not until the introduction of the autoshaping paradigm that these "other features" of the conditioning situation (eg. species-typical behaviors) that could influence response form were systematically investigated.

When Brown and Jenkins (1968) first reported that by simply pairing brief illumination of a response key with the presentation of a reinforcer pigeons would reliably begin pecking at the key, their original interpretation of autoshaping invoked Skinner's (1948) description of "adventitious" reinforcement of responding. Soon various authors (see Hearst and Jenkins 1974; Schwartz and Gamzu 1977 for reviews) began to challenge this notion that keypecking in the autoshaping situation was "superstitious" behavior produced by adventitious reinforcement of orientation to the keylight. Instead, the association of the keylight (signal) with reinforcement was emphasized and the autoshaping keypeck was suggested to be the outcome of a Pavlovian conditioning process. It was in this context that Jenkins and Moore (1973) conducted their study of the form of the pecking response in autoshaping situations and confirmed Wolin's findings concerning the form of keypecks engendered by food and water reinforcement.

While Jenkins and Moore were primarily concerned with resolving the question of whether operant or Pavlovian processes control the emergence of the keypeck response in autoshaping with pigeons, this study can also be viewed as examining how certain exteroceptive stimulus variables (signal-contingency - signals predicting either food or water reinforcers independent of responding) and interoceptive state variables (hunger vs. thirst) interact to determine a behavioral outcome (signal directed pecks of a particular form). Unfortunately, the interpretation given the results of this study was constrained by the paradigms within which the data were interpreted (ie. stimulus substitution as the process underlying Pavlovian conditioning), and bound by the question asked (Is keypecking in the autoshaping situation the result of Pavlovian or operant contingencies?). As a result these authors arrived at the conclusion that the resemblance between the signal directed and consummatory response was a consequence of the contingent relationship between the signal and the presentation of the reinforcer (Pavlovian conditioning). It was recognized that the pecking response of autoshaping differed from the classical reference experiments of Pavlovian conditioning by involving a skeletal movement directed toward the signaling stimulus rather than the elicitation of a local, specific reflex. It was therefore proposed that 'object-substitution' might better describe the observed resemblance between behaviors directed at the signal and those directed at the reinforcer. In this formulation the signal-object in the autoshaping situation comes to act as a surrogate for the reinforcer-object, so that the animal literally re-directs the normal consummatory response to the signal stimulus. Although the stimulus properties of the signal were not varied, it was also suggested that the physical properties of the stimulus might influence response form.

While these conclusions provide a reasonable account of the similarity between autoshaped and consummatory pecks, it should be noted that there was no direct attempt to measure response form. The lack of sensitivity of the subjective dependent variable used to assess response form in the Jenkins and Moore study would undoubtedly obscure anything but gross, qualitative differences between conditioned and consummatory pecks. Comparisons were made on the basis of ratings taken from judges' opinions of whether filmed pecks (events lasting only several hundred milliseconds) resembled instances of eating or drinking. Since these were ratings of the entire sequence, there was also little basis to consider whether specific elements of these patterns were differentially altered or which features of the peck the judges were responding to. Even the measures of force (recorded on a polygraph with a slow paper speed) provided only qualitative differences between food (higher force) and water (lower force) reinforced pecks. Thus, while the difference in form between water and food reinforced keypecks is apparently real, these observed differences are based on qualitative, subjective evaluations that leave the equivalence of conditioned pecks to consummatory responses open to question.

Subsequently, an alternative account of this relation between conditioned and consummatory behaviors was provided by Woodruff and Williams (1974, 1976). Based on evidence that when swallowing only was elicited by water reinforcers presented directly into the beak, pigeons would show the entire appetitive-consummatory sequence directed to the signal, these authors concluded that stimulus-substitution through Pavlovian conditioning was an inadequate explanation of their observations and proposed a "learned release" hypothesis. This theory suggests that autoshaping represents the learned release of phylogenetically and neurally preorganized "relatively fixed action patterns" that constitute innate appetitive-consummatory behavior patterns for feeding and drinking. It was further suggested that such autoshaping phenomena may reflect a developmental process by which the young organism identifies biologically significant stimuli in the environment and comes to respond with appropriate species-typical approach and ingestive behaviors (Woodruff, Morrison and Williams, 1974; Woodruff and Starr, 1978).

Although this account may be satisfying as an explanation of why signal-directed behavior during autoshaping should occur at all, and what the adaptive significance of this sort of associative learning might be, invoking the concept of a fixed action pattern (FAP) provides little aid in the analysis of the factors controlling the form of this behavior. Since the FAP by definition is a motor pattern that is independent of stimulus control once elicited (Hinde, 1970), and usually requires a mechanism involving genetic determination via central neural organization, it is doubtful that the motor patterns produced in autoshaping situations will conform with this traditional view. It may be stressed that the FAP is best used as a descriptive classification rather than an explanatory principle for the mechanisms controlling behavior; and so even within the learned-release paradigm the analysis of how these species typical movement patterns are organized is still unresolved.

It is worth mentioning that a variety of studies have reported a resemblance between signal directed behaviors and those typically controlled by the reinforcer with other zoological species such as dogs (Smith and Smith, 1971), goldfish (Bottjer, Scobie and Wallace, 1977; Woodward and Bitterman, 1974), archer fish (Waxman and McCleave, 1978), Talapia (Squier, 1969), young chickens (Woodruff and Starr, 1978) and rats (Peterson, Ackil, Frommer and Hearst, 1972; Steirs and Silberberg, 1974; Myer and Hull, 1974; Hull, 1977). Autoshaping studies reporting only partial or no resemblance between signal and reinforcer elicited behaviors include investigations with rats under omission training (Atnip, 1977), rats with the presentation of another rat as the signal (Timberlake and Grant, 1975) or electrical brain stimulation as the reinforcer (Wilkie and McDonald, 1978), chickens with heat as the reinforcer (Wasserman, Gutowski and Bader, 1975), squirrel or rhesus monkeys with food reinforcers (Gamzu and Schwan, 1974; Sidman and Fletcher, 1968), and mentally retarded humans with food reinforcers (Kagain, Anson and Sperber, 1976). In these studies it was often pointed out that the unconditioned behaviors elicited by the reinforcer were quite variable and that for these species the physical properties of the signal or manipulandum would provide an additional influence on response form.

While there appears to be little doubt that the relation between signal and reinforcer is primarily responsible for the emergence of signal directed behavior in an autoshaping situation, the problem remains that it is quite possible that there are multiple factors operating in the control of this seemingly simple response system. It may be more advantageous to consider such behavioral phenomena within a framework that can allow more than just a single process to be operate (e.g. stimulus substitution or learned release of an innate FAP). This also gives rise to a larger question concerning the integration of the diverse motivational factors composing behavioral context to produce a behavioral output. At issue is whether there really are dichotomous, either/or, classes of pecks (as would seem to be suggested by the approaches of Jenkins and Moore or Woodruff and Williams) or do different factors go together in such a way as to provide a continuous transition from one response form to another along a continuum. It is quite possible that when various response systems are examined some will fall in the first category (discrete) and others will fall in the second (continuous). Similarly, within a given motor sequence certain elements may be relatively fixed, representing a repertoire of stereotyped behavioral subroutines, while others may show variability in form, reflecting different sources of control and capacity for continuous variation. Consideration of the mode of selection among a variety of response topographies as various putative controlling variables are manipulated would seem an essential step in the analysis of any movement pattern.

Investigations of the control of pecking topography by operant contingencies also provide data relevant to these questions of: (1) how are individual behavioral elements integrated into complex motor patterns, and (2) do different features of response form show capacity for modification independently of one another. The procedure for response differentiation through differential reinforcement has a long experimental history (Ferster and Skinner, 1957; Notterman and Mintz, 1965). An early study by Skinner (1958) reported success using contingent reinforcement to increase the force with which pigeons pecked keys. Although the pigeon's keypeck was to become the 'prototypical' operant response, it was not for some time (and the advent of competing Pavlovian interpretations of keypecking) that detailed investigations of operant keypecking topography were to appear.

The study by Rilling, Kramer and Askew (1970) provided a good description of the dynamics of the pigeon's keypeck and is most notable for the development of a pecking key that incorporated a force transducer to provide a continuous voltage analog representation of response force during key contact. By storing the waveform of individual pecks on an oscilloscope, accurate measures of peak force and duration were obtained. Two sorts of wave forms were typically produced; single unimodal peaks lasting 5 to 15 msec, or bimodal waveforms with the first peak higher than the second and longer durations of 20 to 50 msec (or two short durations if the waveform crossed zero force between the peaks). The average force of keypecks produced by continuous reinforcement (CRF) was reported to be 100 - 250 grams. No attempts to control force or duration by differential reinforcement were made in this study.

In 1972 Schwartz and Williams examined pecking response durations during autoshaping, negative automaintenance (an autoshaping procedure in which responding eliminates reinforcement delivery) and operant procedures (fixed interval, fixed ratio); and then attempted to alter response durations through duration-contingent differential reinforcement. All procedures initially supported short duration keypecks, but with autoshaping and operant schedules a population of long duration pecks emerged and eventually predominated. Birds on negative automaintenance continued to produce only short durations. When only short duration or long duration pecks produced food reinforcement only the relative frequency of longer duration pecks was increased. This finding, that short duration keypecks were apparently insensitive to operant contingencies, led Schwartz and Williams to suggest that there were two basic types of keypeck that could be distinguished on the basis of duration. Since responding under negative automaintenance was presumably maintained only by the signal-reinforcer association, short duration pecks were viewed as the outcome of a Pavlovian process and derived from the pigeon's species-typical feeding response. Longer duration pecks (greater than 25 msec) were presumed to be under outcome-contingent (operant) control. This two-process classification was then used to account for the distribution of response durations obtained in a variety of operant schedules (Schwartz, 1977a; Schwartz, Hamilton and Silberberg, 1975). Unfortunately, the conclusion that short durations were more representative of feeding was not based on any examination of the pigeon's feeding topography. Moreover, all of the mean response durations reported by Schwartz and Williams were on the order of two to four times greater than those reported by Rilling et.al. (1970).

Another study by Schwartz (1977b) provided additional support for the two-process interpretation of keypeck duration. In this study pecking was maintained on a variable interval schedule of reinforcement and attempts were made to suppress the relative frequency of long or short duration pecks by duration-dependent electric shock. The failure to alter the relative frequencies of response durations when short durations were punished, as opposed to a reduction in the frequency of long duration pecks when long durations were punished, was again interpreted as evidence for two classes of conditioned pecks that differed in their sensitivity to response-contingent control. It is a weakness of this study that it did not provide an adequate control for the number of shocks received during the two punishment conditions (during the short-duration shock condition only about 10% of the total responses were followed by shock, while during the long-duration shock condition about 50% of responses produced shock). Furthermore, because the effect of response contingent shock was to suppress responding (and perhaps lower response force), then for those responses obtained under either of the punishment conditions short durations might be expected if shorter durations are associated with less vigorous (forceful) keypecking. In discussion it was acknowledged that different response durations might actually reflect changes in some other aspect of response topography (force was suggested), but it was concluded that whatever the correlated change in topography underlying duration might be, two classes of peck could nevertheless be distinguished on the basis of control by contingent reinforcement.

The possibility that a variable such as force might determine the response durations observed in these studies provides an alternative explanation of these data. Smith (1974) examined pigeon's operant pecking topography utilizing a high-speed photographic technique. Smith reported that pigeons typically made key-contact with the beak open and then, 15-30 msec after contact, closed the beak with a lateral movement on the key. Depending on the physical properties (activation force) of the response key, this lateral movement could produce either two short duration responses with a 30 msec interresponse time, or a single longer duration response. Further, studies of differential reinforcement of short interresponse times indicated that pigeons typically did not alter the form of the pecking response, but altered the locus and angle of key contact in order to increase the likelihood of producing short or long durations. There was no evidence for two topographically distinct classes of long and short duration pecks. Apparently the pigeons were not only sensitive to duration-dependent operant contingencies, but could take advantage of certain characteristics of transduction devices to meet such contingencies.

In 1978 Ziriax and Silberberg provided additional evidence that pigeons can both discriminate and emit different keypeck durations. The ability to discriminate peck duration was demonstrated by a conditional-discrimination procedure in which the birds first pecked, then indicated the duration of the peck by choosing the appropriate comparison-stimulus color for subsequent responses. After birds were trained to choose colors to indicate peck duration, key colors were used as discriminative stimuli signaling reinforcement of long or short duration pecks. In this situation birds produced more short duration pecks when short durations (10-20 msec) were reinforced, but had difficulty making sufficiently long duration pecks when the reinforcement criteria was greater than 100 msec. These authors concluded that keypeck duration was sensitive to operant contingencies and went on to propose that peck duration was positively correlated with "response strength" under circumstances where reinforcement was not directly contingent on response duration. Unfortunately the only dependent variable available to represent response strength was response rate; and it is not immediately apparent why duration should increase as response rate increases unless an additional variable such as force was also correlated with rate.

Two recent studies provide further evidence that pigeons' keypeck duration can be altered by differential reinforcement schedules (Zeiler, Davis and DeCasper, 1980; Whipple and Fantino, 1980). These studies also used commercial microswitch-type response keys for timing duration and were only able to demonstrate small changes in mean response duration in the direction of the reinforcement criteria. It is perhaps more important to recognize that in all of these attempts to control peck duration by operant contingencies terminal performance has been only marginal, with many responses occuring outside the reinforcement criteria. The study by Zeiler et. al. is particularly important in this respect because they found that as the duration requirement was increased, mean response duration increased only slightly but the standard deviations of response duration increased more rapidly. Apparently it is rather difficult to get pigeons to respond with a motion other than a ballistic impact for food reinforcement, making responses involving sustained contact longer than about 100 msec very rare (cf. Jenkins and Moore (1973), Woodruff and Williams (1976) concerning durations of water reinforced pecks). It is therefore likely that the durations reported in all of these studies do not reflect operant control of duration per se, but variations in other aspects of topography (e.g. force, angle of contact) that by interaction with the physical properties of the transducer produce different durations. It should further be recognized that the effectiveness of response differentiation procedures in altering response duration (or some other correlated feature of topography) appears to be limited to changes occuring within a range specified by the form of the pigeon's natural pecking response appropriate to the reinforcer. For pigeon's keypecks it seems that operant contingencies can alter topography within a given mode of responding, but cannot produce an entirely different form of response (e.g.

ballistic pecks changing to a pressing motion involving sustained contact).

It is clear that many issues remain unresolved concerning the control of response form in conditioning situations and the relationship between conditioned and consummatory responses. The pigeon therefore provides a useful preparation to study the multiple determinants of response form. It is also convenient that the neural control of some of the anatomical structures in service to these responses has been examined and seems to constitute a relatively simple neuromuscular system (Zeigler, 1976, 1980; Zweers, 1974). A behavioral preparation that would lend itself to the study of the neural control of several different behavioral outputs from the same muscle groups would be invaluable. As Dawkins and Dawkins (1973) have pointed out, it is only with a fine-grain spatiotemporal description of a particular motor pattern that the neurophysiologist will have tangible units of behavior to explain. Thus, reexamination of the factors governing pecking response form in the pigeon can provide a description of how diverse inputs combine to produce a behavioral output, as well as a behavioral preparation from which to examine the neural control of these behavioral processes. Such an analysis requires precise, quantitative dependent variables with which to characterize the form and variability of these responses and an experimental design that allows independent control of a variety of putative causal variables.

Experimental Design

Because the movements mediating feeding and conditioned responding involve continuous changes in topography over time, the moment of substrate contact was chosen as an unambiguous temporal landmark that would allow comparisons between various movement patterns. As can be seen for the feeding response in Figure 1, at the moment of contact behavioral endpoints are reached for three response elements: beak opening (gape), eye closure and the spatial localization (trajectory) of the peck. The peak force and duration of contact provide additional quantitative measures of response topography. Since it was desirable to measure the form of feeding and conditioned responses in situations as similar as possible, both feeding and conditioned pecks were directed to a floor-mounted response key. Feeding topography was measured by placing seeds directly on the response key so that pecks would activate the transduction devices. For conditioning situations the response key served as a visual signal and manipulandum. Table I lists the five dependent variables used to characterize response topography, together with the independent variables that were considered to have putative roles in the determination of response form. With these independent variables it was hoped to influence both interoceptive state variables and exteroceptive stimulus variables. The stimulus control of feeding topography was examined by allowing the pigeons to eat seeds of different sizes. In conditioning situations the effect of changes in the stimulus properties of signals was evaluated by providing various sorts of signal targets. The stimulus properties of the food reinforcers was also manipulated, as well as the contingencies between signals, responses and reinforcement.

Methods

Subjects

Subjects were ten male, White Carneaux pigeons (Columba livia) obtained from the Palmetto Pigeon Plant, Sumter, S.C. All pigeons were maintained at approximately 80% of free-feeding body weight with a daily ration of approximately 20 grams of milo (a 3-5 mm diameter seed).

Apparatus

The experimental chamber was 30 cm by 38 cm and 42 cm high, with a wire grid floor. One wall and the ceiling were clear Plexiglas and the remaining walls were painted flat black to reduce reflection. In a corner next to the Plexiglas wall a 25 mm square response key was mounted in the floor 4 cm away from the adjacent walls. The opening to a grain hopper (Lehigh Valley Inc.) was centered 3 cm above the floor on the black wall adjacent to the response key. For photographic purposes the chamber was enclosed in a small light-proof room. Chamber illumination was provided by a safelight (15 watt bulb) with a Kodak 1A red filter mounted one meter above the chamber.

The pecking surface of the response-key was frosted acrylic allowing rear-projection of various signal stimuli.

The response key incorporated a Lafayette Instruments Force Transducer (#76613) that produced a continuous voltage analog of applied force during key-contact. The voltage output of the force transducer was calibrated for both static and dynamic forces (different weights were either placed on the key or dropped from 10 cm above the key). This signal was monitored by a voltage comparator that provided response onset-offset logic pulses for responses that exceeded a force threshold of 10 grams (see Appendix for details of the design of the response key, associated instrumentation and projection system). Response duration was timed to the tenth of a millisecond by a Hewlett-Packard Universal Counter (#5325B) and printed by a Hewlett-Packard Digital Recorder (#5050B). The analog signal from the force transducer was displayed on an oscilloscope (Tektronix Type 564) triggered by peck onset, and each peck waveform was photographed by a Grass Instruments C-4 Kymograph Camera. A microfilm reader was used to obtain measures of peak force from the photo-negatives. Scheduling of experimental events was accomplished with Lehigh Valley Inc. solid state programming equipment located in an adjacent room.

The photographic system used to obtain a size-calibrated image of the pigeon at the moment of key-contact utilized a Photographic Alliance 35mm Instrumentation Camera (#0001) with a Nikon 55mm macro lens and a General Radio strobe light (#1539A). Because of the delay imposed by shutter-opening (about 10 msec) and the limited film capacity of conventional reflex-type cameras, a shutterless camera was used with Kodak 2495 Orthochromatic Film (blue sensitive, 35mm X 150 ft). This film was not exposed by the ambient red light from the safelight and exposures were obtained by a 5 microsecond flash of the strobe. The strobe was activated by a solid-state relay (1 microsec activation time) controlled by the voltage comparator so that the precise moment of key-contact was reliably photographed. Data for gape (distance between peak tips), eye opening (distance between eyelids), and location of each peck was taken from the photo-negatives on a Realistic Microfilm Reader with 22X magnification. Because the camera required 0.8 sec to advance one frame, any pecks occuring during the film advance period were not recorded.

Procedure

All subjects were hopper-trained prior to the experiments and then five birds were randomly assigned to the autoshaping and operant groups.

Autoshaping. The autoshaping schedule consisted of a 1 min variable intertrial interval with a 6 sec signal followed by 4 sec access to food independent of responding. Availability of food was signaled by hopper illumination. Each session consisted of 40 signal-food trials except those in the dot-stimulus condition which had 42 trials. Table II lists the training each subject received. Acquisition training was conducted with a signal that consisted of illumination of the key (plain signal) and milo reinforcer (3-5mm seeds) for a sufficient number of sessions to record at least 100 pecks for each subject. Two birds that failed to respond within 3 sessions were replaced as subjects. Training continued with sessions in which signals consisted of circular stimuli (2,4,6,10 and 14mm diameters). One session was run with black dots on a white illuminated background, and another session with white dots on a black background. During each session all dot sizes and a plain signal appeared seven times in random order. Two sessions were run with a plain signal and dried peas (5-8mm diameter) as the reinforcer. For the seed-key condition a 5 mm diameter seed was glued to the center of the response key, signals consisted of illumination of the key and milo served as the reinforcer. When all conditioning sessions were complete, each subject was allowed to eat seeds placed on the key. Several seeds of a single type were placed on the key, and when they were eaten, several more replaced until at least 20 pecks for each seed type were recorded. Milo (3-5mm) was given first, followed by peas (5-8mm), and then garbanzo beans (9-12mm).

Operant. The birds in the operant group were shaped by the method of successive approximations (Segal, 1972) to peck the illuminated response key (discriminative stimulus or signal) to obtain 4 sec access to milo. Reinforcer delivery terminated key illumination. When the key was dark, responses were without effect. Initially during shaping the key was illuminated continuously and periods of key illumination were progressively decreased until signal onset reliably controlled responding. The shaping procedure typically required two sessions and was terminated after 15 successive signal illuminations with a response.

Table II lists training conditions for the operant group. The signal stimuli, reinforcers and trials per session were the same as those described above for the autoshaping group. As pecking was acquired, birds were placed on a discriminated CRF, 6 sec limited hold, variable intertrial-interval 1 min reinforcement schedule (Disc CRF, L.H. 6 sec, VITI 1 min). In order to match both rate of response and density of reinforcement with that of the autoshaping group, the schedule was next changed to a Disc VR3, L.H. 6 sec, VITI 1 min. This schedule was in effect while another 100 responses to a plain key were recorded and throughout the sessions in which signal stimuli and reinforcer type were manipulated. In a final extinction session, after ten reinforced trials the key was illuminated continuously and responding no longer reinforced. This session continued until a criteria of 100 responses or 30 sec without a response was reached. When all of the conditioning sessions were complete, eating data for different seed sizes were recorded in the same way as described for the autoshaping group.

Results

Comparison of the form of the movements mediating feeding and conditioned responding indicates that while certain elements of topography are quite similar and seem to reflect the same sources of control, other features of these response patterns such as the force of contact and stimulus control of peck location are quite different. In Figure 2 group means and standard deviations for force, duration, gape (distance between beak tips) and eye closure (distance between eyelids) are presented for feeding and conditioned responses. The group means were obtained by averaging the means for each of the five subjects in each conditioning group. The conditioned responses were recorded in the autoshaping and operant VR3 conditions with a plain key and milo reinforcer. The combined feeding response data for each group are shown for comparison. The values for gape during feeding were restricted to eating pecks directed at milo. It can be seen that neither closure of the eye nor gape differed substantially for any condition. The mean distance between the eyelids ranged between 1.6 mm and 2.0 mm, and the mean distance between beak tips ranged between 4.8mm and 5.7mm. Thus, the eye was typically closed or nearly so (when the eye is fully open the distance between the eyelids is about 10 mm), and the beak was open at the moment of contact. These common features of feeding responses and conditioned keypecks can be seen clearly in the photographs presented in Figure 3. By contrast, means for the force and duration of conditioned keypecks were greater than those obtained for feeding responses. For the autoshaping group a mean keypeck force of 88.5 grams compares to a mean contact force of 44 grams during feeding. With the operant conditioning group a mean keypeck force of 79 grams versus a feeding mean contact force of 38 grams was obtained. The statistical analysis summarized in Table III confirmed the fact that the difference in force between feeding and conditioned responses was significant. The observed differences in contact duration failed to reach significance because of the greater variability associated with this measure.

The data in Figure 2 also indicate that there were no statistically significant differences in keypeck response form between the autoshaping and operant groups. The group means for response form on the operant CRF and VR3 schedules were also quite similar; although the analysis of the data for individual subjects that is summarized in table IV shows that some birds did show statistically significant changes in response form between the two schedules. However, the direction of such individual changes was not consistent across subjects for any measure. The effect of the extinction schedule was a significant increase in the mean response force of four of the five subjects (table V). Examination of the raw-data for extinction reveals that the slight elevation of the means was a consequence of occasional pecks of substantially greater than normal force. Increases in the vigor and variability of responding are consistent with previous descriptions of responding during extinction (Ferster and Skinner, 1957). Taken together, these results suggest that when other features of the conditioning situation such as reinforcer type (food vs water) are held constant, response-reinforcer contingencies that do not constrain response form by imposing an explicit topography-reinforcement relationship tend to produce conditioned movements of a rather characteristic form.

In order to further examine the stereotypy of feeding and conditioned responses, means and standard deviations of individual subjects were plotted in Figure 4 for the same measures of response form shown in Figure 2. The conditioned response data are again from the autoshaping and operant VR3 conditions with a plain signal and milo reinforcer. It is apparent that for both feeding and conditioned responses there was moderate response variability both within and between subjects. However no subject's mode of response was entirely different and there was noticable within-subject consistency, particularly with regard to force where several subjects' means indicated characteristic differences.

The relationship between the force and duration of conditioned keypecks is shown in Figures 5 and 6 which plot force in grams as a function of duration in msec for individual responses recorded in the autoshaping and operant VR3 conditions with a plain signal and milo reinforcer.

The points in Figure 5 form two distinct populations; most of the responses were between 3 and 20 msec with a small proportion of pecks between 30 and 50 msec. The lower range of duration exhibits a positive correlation with force. The set of responses with longer duration does not appear as a continuation of the force-duration relationship that characterized the short duration responses, although all of the responses above 30 msec were of medium to high force. The solid line in Figure 5 shows the relationship between the force and duration of ballistic impacts produced by dropping different weights from 10cm above the key. The slope of this line also indicates that as the force of impact increased, longer durations were produced. This relationship was apparently the result of increasing physical displacement of the key as the force of impact increased, with the particular slope determined by the physical characteristics (fall-time) of the transducer. Comparison of the slope of the line and the plotted positions of the majority of pecks suggests that most of the key-contacts were ballistic in nature with durations determined by the force of impact. It is of interest to note that nearly all of the 30 to 50 msec response durations were produced by a single animal (see #249, Figure 4). This bird characteristically made high force pecks and was observed to strike the key at a slight angle so that beak contact involved a lateral movement on the key (a lateral movement during keypecking involving a rostral to caudal head rotation as the beak closes was also reported by Smith, 1974). In Figure 6 a similar high positive correlation between the force and duration of operant keypecks is readily apparent, but in this case only three responses occurred that were greater than 30 msec duration.

Additional support for the view that many keypeck durations were primarily determined by the force of impact and physical properties of the transduction system (activation force threshold and return characteristics) is provided by Figure 7 which shows three typical force-time records for pecks obtained in these experiments. The uppermost waveform typifies the vast majority of responses: It consists of a single peak that is relatively symmetrical. It can be seen from the shape of this waveform that as the height of the peak (force) increases, the width at the base (duration) will gradually increase. The middle waveform was the second most common. It has a bimodal shape with the first peak higher than the second. Between the peaks, the waveform crosses the force threshold value so that only the duration of the first peak was measured in these experiments. Together these two waveforms make up the population of pecks for which force and duration were correlated. The bottom waveform shows how the longer durations were produced. Long duration pecks also typically produced a bimodal waveform, but in this case there was often substantial force and duration was recorded to the end of the second peak. Careful consideration of Smith's (1974) photographic analysis of pecking topography suggests that this second peak is produced during the beak closing that often follows key-contact as part of the food-reinforced conditioned response.

Relative frequency distributions for peck duration, in 2 msec class intervals, are shown in Figures 8 and 9 for the autoshaping and operant VR3 conditions. Both distributions are fairly symmetrical, peaking at the 8-10 msec interval for the operant group and the 10-12 msec interval for the autoshaping group. The duration distribution from the operant condition shows somewhat less variation, and both distributions show a slight skew toward shorter duration values. The most notable difference is the occurance of a small proportion of responses in the interval between 36 and 44 msec for the autoshaping group. As stated previously, these long durations were primarily responses of a single animal and were sufficiently infrequent that there was little effect on the autoshaping group mean for duration. Thus, there was no evidence that operant and autoshaping contingencies produce different response topographies that could be distinguished on the basis of duration.

In summary, the data for force and duration indicate that conditioned keypecks for grain reinforcement consist of a rapid, ballistic key contact of substantially greater force than normally occurs with responses directed at food. Most of the duration values measured in this study were primarily determined by the force of key-contact and keypeck duration did not serve to distinguish between conditioning paradigms.

The control of peck location provided another contrast between feeding and conditioned responses. Before considering conditioned keypecks, it should be pointed out that pigeons exhibit remarkably consistent accuracy in directing feeding pecks to seeds. (Zeigler et.al., 1980) The control of peck trajectory must apparently be pre-determined on the basis of visual and proprioceptive information before rapid downward movement starts, because the eye begins to close soon after head-descent is initiated. Since the visual stimulus plays a crucial role in determining the location of feeding pecks, the effect of providing various sorts of targets in conjunction with the visual signal of the conditioning situation was examined. Black dots of different sizes were projected on the key with a white illuminated background and these stimuli can be considered signals with targets. For white dots on a dark background the target was the signal. (The floor surrounding the key was painted black.) Since the targets were projected uniformly in the center of the response key, from the photograph of each peck it was possible to record those responses for which the beak-tip contact was centered over or on the key-targets. Figure 10 shows the percentage of pecks that were directed at the black and white dot targets by the autoshaping and operant groups. It is apparent that both groups directed a substantially greater proportion of pecks at the white dot stimuli, although the control of peck location was far from perfect. For the autoshaping group 34% of the total responses in the white dot condition were located on the target, while 17% of the responses were on target in the black dot condition. For the operant group stimulus control by white dot stimuli was better, with 55% of responses on target compared to only 5% of responses on target in the black dot condition. A logit analysis for categorical data (Grizzle, Starmer and Koch, 1969) confirmed that there was a significant difference in responses on target for the black and white dot conditions (chi-square = 50.79, $P < .0001$), as well as a significant group by dot interaction (chi-square = 15,89, $P < .0001$). The significant interaction indicates that while both conditioning groups directed more pecks at the white-dot stimuli, the relative magnitudes of the black vs. white dot differences were also statistically different between the conditioning groups. Further analysis of the data from the white-dot condition revealed that the difference in the percentages of responses on target for the autoshaping and operant groups (34% vs. 55%) was statistically significant (chi-square = 16.41, $P < .001$), although such a quantitative difference between the conditioning groups should perhaps be considered tentative with only five subjects per group. These results indicate that pigeons will direct pecks at localized signals (the white dots) in conditioning situations, but stimulus features of signals (black dots) are not treated as targets for peck location.

In order to provide a signal-target with stimulus properties more similar to food stimuli, conditioning sessions were run with a seed glued to the center of the response key. This provided a three-dimensional target with visual stimulus properties identical to food. The conditioning signal continued to be the illumination of the response key. Figure 11 shows the percentage of birds in the autoshaping and operant groups that pecked at the seed for the first 15 successive pecks recorded in the session. In both groups the birds initially pecked at the seed, but across successive responses the number of birds making contact with the seed declined. By about the eighth peck the birds no longer treated the seed as a target, typically pecking around the seed on the periphery of the key. The forces of keypecks in the seed-key condition, for pecks both on and off the seed, were within the typical range for conditioned keypecks with a plain signal and did not vary systematically during the session. There was also no apparent difference in beak opening for pecks on and off the key. It is also important to note that the number of pecks was undiminished by the failure to ingest the seed, only the location of pecks was altered. This sort of outcome-contingent control seems to indicate that at least one feature of the pecking response, peck location, requires appropriate proximate feedback of a seed in the mouth to be maintained, while the propensity to peck can be maintained by delayed feedback provided by subsequent access to grain.

Another aspect of the pecking response that was expected to be controlled by visual stimulus properties was gape. The photograph of the pigeon's feeding peck in Figure 3 shows that the extent of beak opening at the moment of seed contact is a distance slightly greater than the size of the seed. The data in Figure 12 confirm that across a range of seed sizes beak opening at the moment of seed-contact is proportional to the diameter of the seed. Figure 12 plots gape in mm as a function of seed diameter in mm for individual feeding responses from all ten subjects. The diagonal line shows the inter-beak tip distance necessary to match various seed diameters. Points falling below the line indicate pecks for which beak opening was insufficient to grasp the seed. It is clear that gape increased as seed size increased and that for the majority of pecks, beak opening was slightly greater than the seed diameter. However, there was a substantial number of pecks on which beak opening was less than seed diameter and the relative proportion of these errors increased with greater seed size.

The finding that responses with beak opening smaller than seed diameter increased in frequency with larger seeds was further investigated by examining the relationship between gape and seed size across successive pecks. Figure 13 shows the mean difference (error) in mm between gape and seed diameter for successive blocks of two pecks from eight birds. Means for eating three sizes of seed are shown.

Milo ranging from two to four mm in diameter was tested first and for all birds the size of beak opening was greater than seed diameter for nearly every peck. Milo was the only food given in the home cage, so the birds had extensive experience eating seeds of this size. Five to seven mm peas were tested next and many animals made errors (gape less than seed size) during the first several responses, but within three to four pecks beak opening was adjusted and few errors were made thereafter. Following the peas, the birds were given 9-12 mm garbanzo beans to eat. For this large diameter food nearly all birds made errors initially as shown by the mean negative value for the first block of pecks, followed by a gradual rise reflecting increased gape across successive pecks. Only in the final block (pecks 9-10) did the mean error for the largest seeds reach a positive value equivalent to the smaller seed types.

Examination of the factors controlling gape in conditioning situations provided good evidence that gape, by comparison to peck force and location, may be a good behavioral element representing the relationship between feeding and conditioned responses. Figure 14 shows mean gape in mm as a function of target size in mm for signals with white or black dot stimuli. Data for both autoshaping and operant conditioning groups are given. For the autoshaping group neither white nor black dots produced any noticeable change in beak opening. In the operant group, gape size was not influenced by signals with black dots, but for the white dot signals there was a slight effect for the smallest and largest target sizes. Although the values for beak opening were not even close to the diameters of the targets, the 2-mm white dots produced the smallest mean gape (4.8mm) and the 14-mm dots the largest (7.7mm). Small differences in gape for 2mm and 14mm targets were apparent for all five subjects in the operant group and therefore statistically significant ($P < .05$, Wilcoxon matched-pairs of signed-ranks test). It is of interest that the operant condition with white dots also had the greatest percentage of pecks on target (see Fig. 10). Considering only those responses on target (about 55% of the total) did not substantially improve the relationship between gape and target size, indicating that peck location and gape were not correlated. Thus, it appears that the visual stimulus properties of signals in conditioning situations do relatively little to influence pecking response form.

Although beak opening of conditioned keypecks did not appear to be under visual control, change in the size of the seeds given as reinforcement resulted in a significant change in gape. Figure 15 presents group means for gape in mm for responses obtained with milo or pea reinforcers in the autoshaping and operant VR3 conditions. For both groups the larger pea reinforcers produced pecks with wider gape. Table VI compares mean gape for each subject with milo and pea reinforcement. It is clear that significant increases were consistent across subjects in both groups. Moreover, the increases in beak opening were of about the same magnitude as the difference in the average size of the two types of reinforcer. Thus for both conditioning groups, the average beak opening was the size appropriate for eating the particular seed given as reinforcement. Considering that in the feeding situation gape also seemed to be adjusted primarily on the basis of the size of seeds previously eaten (eg. Fig. 13), it appears that for both feeding and conditioned responding the determination of gape reflected a set provided by previous experience rather than visual information available before each peck was initiated.

Discussion

It is apparent that detailed, quantitative analysis of the form of the pigeon's pecking response does not support the contention that pigeons possess a highly stereotyped, centrally preorganized consummatory response that normally mediates ingestion of food and secondarily can be redirected to response keys by various conditioning paradigms. What can be said is that the movements mediating feeding and conditioned responding bear a strong resemblance to one another. But, to account for why this similarity exists, it is not necessary to invoke a unitary behavioral construct for both behaviors like the release of a common feeding fixed action pattern or elicitation (substitution) of an unconditioned (feeding) response. The results of this study clearly show that both feeding and conditioned responses are composed of several behavioral elements, each of which may reflect several potentially independent sources of control. An understanding of the similarities and differences between these behaviors requires an analysis of the proximate causation underlying the organization of these behavioral elements into specific movement patterns. Both feeding and conditioned movements involve a pecking response and therefore utilize the same effector systems (eg. muscles of the jaw controlling gape, muscles of the neck controlling peck location, etc.). Moreover, each effector system must depend upon a central neural organization that will undoubtedly further constrain the possibilities for different behavioral outputs. Finally, both movement patterns may share similar sources of control by stimulus input for guidance and orientation. These may be external stimulus factors or response-produced sensory beedback. Thus, without detailed analysis of the underlying mechanisms, the organization and control of the movements composing these behaviors remains unresolved.

The control of eye closure provides an example of an element that was common to both feeding and conditioned responses. Although equivalent eye closure during the peck was seen in both behaviors, several observations suggest that eye closure was apparently the result of the rapid acceleration of the head produced by both movements. First, the eye can be observed to close during rapid withdrawal of the head from the substrate, indicating that eye closure is not necessarily a visual reflex response to the rapidly enlarging image produced by downward movement of the head as suggested by Zeigler et.al. (1980). In addition, the eye also closes during the head-descent phase of the pigeon's drinking response (Klein and LaMon, 1981). It therefore seems more likely that eye closure is the result of a reflex to stimulation of the vestibular system produced by rapid head acceleration. Thus, although temporaly correlated with pecking responses, eye closure does not share a common causation related to feeding; but rather was elicited independently by movement-produced stimulation common to both feeding and conditioned responses.

Another behavioral element that appeared to have a similar source of control in both conditioned keypecks and feeding was beak opening. The finding that a change in seed size during feeding did not result in an immediate adjustment of beak opening on subsequent pecks was somewhat surprising evidence that, contrary to the statements of Zeigler et.al. (1980), gape is not primarily or exclusively under visual control. It appears that the size of seeds previously eaten provided a reference for the determination of gape during feeding, either by influencing the calibration of the sensory-motor transform mediating visual stimulus input to gape output, or by directly affecting gape through a link between somatosensory information and beak opening on subsequent pecks. In the conditioning situation, similar factors appeared to determine beak opening for keypecks. Visual target stimuli presented with conditioning signals had a very minimal influence on gape, while a change in the size of the reinforcer not only resulted in an equivalent change in gape, but seemed to produce keypecks with the extent of beak opening appropriate for eating the particular size reinforcer. These findings indicate that beak opening during feeding and conditioned keypecking was not primarily under proximate (visual) stimulus control, but reflected a set (expectancy) determined by the size of the food previously ingested.

Just as common stimulus factors (eg. head acceleration) produce certain similarities in the form of responses produced in different behavioral contexts, differences in orienting stimuli and response-produced sensory feedback can be expected to result in contrasts in response form. The substantial difference in the contact force of conditioned keypecks and feeding responses may be at least partly attributable to such differences. The feeding peck is directed to a stationary, three-dimensional object and typically results in the appropriate intra-oral somatosensory information from food that serves as the coordinating link for initiating the subsequent grasping, mandibulation and swallowing elements of the feeding response sequence. The conditioned keypeck is directed to a flat, two-dimensional illuminated surface and does not produce the same sensory feedback as food in the mouth. Thus, the substantial increase in the force of conditioned keypecks may result from the difference in the object to which the peck is directed and the failure of the pecks to produce appropriate sensory feedback.

Unfortunately this interpretation cannot be the complete explanation for why the form of conditioned keypeck should be different from the eating peck, since it should not be assumed that the pigeon is literally trying to eat the key (although in some sense this is what Jenkins and Moore (1973) and Woodruff and Williams, (1976) were proposing) and even high force pecks are no more effective in producing proximate oral food stimuli. The fact that the propensity to peck remains undiminished under circumstances where the immediate outcome of responding is not like that of eating suggests that the conditioned keypeck is more than a misguided feeding response and may reflect in part a natural tendency to interact with signals for impending food stimuli. This is exactly what is required of the animal in the operant conditioning situation. The autoshaping paradigm may also provide a situation in which the animals' signal contact serves an exploratory role, since it would certainly be adaptive to investigate stimuli that reliably predict the availability of food. In this case the conditioned contact response may be described as having an appetitive function in the original sense of food-seeking (Craig, 1918); and this reaffirms the fact that the conditioned response is not feeding. Thus, the responses obtained in both autoshaping and operant conditioning situations may be as much 'signal appropriate' appetitive behavior as 'reinforcer appropriate' consummatory behavior that has been redirected to (or elicited by) the signal.

The control of peck location provided another element of response form that served to differentiate feeding and conditioned responses. Since the feeding peck functions as a means for making contact with food prior to ingestion, consistent and accurate orientation of peck location by food stimuli is a necessity. By contrast, orientation to the target stimuli associated with signals was not a requirement of the conditioned response and was never reliably exhibited. The number of pecks located on the black dot targets was no more than would be expected by chance. The greater proportion of pecks at the white dot stimuli was probably the result of the tendency to peck at a more localized signal, since stimulus control was not consistent and there was no apparent relationship between gape and target size for pecks located on target. The loss of stimulus control of peck location across successive responses in the seed-key condition was the most compelling evidence that for both conditioning groups keypeck location was under outcome-contingent control and that the proximate sensory feedback from keypecks provided adequate information that these were not successful feeding responses. It must again be stressed that only the location of pecks was altered, while the tendency to peck was sustained. Therefore it appears that continued orientation to stimulus features of conditioning signals is not an inherent property of the conditioned response, but rather is dependent on intra-oral response-produced feedback.

This study provided additional data relevant to the issue of outcome-contingent control of response form. The clear relationship between the force and duration of conditioned keypecks suggests that previous studies reporting attempts to manipulate keypeck duration through differential reinforcement contingencies were probably influencing the force of keypecks and not controlling duration directly. This is not surprising since it is unlikely that any neuromuscular system can effectively modulate a skeletal motor response in the millisecond range. The suggestion that peck force through interaction with the physical properties of the response key may have provided a variable that influenced the durations recorded in previous studies is also supported by the rather poor accuracy of the terminal performance reported in those studies that did show success in modifying mean keypeck duration (eg. Zirax and Silberberg, 1978; Zeiler et.al., 1980). Thus, any future studies that examine the pigeon's ability to meet duration-dependent differential reinforcement contingencies should consider whether the modification of keypeck duration results from the adjustment of peck force.

The fact that no significant differences in form were found between keypecks produced in the autoshaping and operant conditioning situations indicates that in the absence of any explicit topography-reinforcement contingency the conditioned responses produced by these paradigms are of remarkably similar form. The operant CRF and VR3 reinforcement schedules also did not produce any systematic changes in response form. These findings are of particular significance since they indicate that the autoshaped keypeck with food reinforcement is no more similar to a feeding response than a keypeck produced by an operant contingency (cf. Schwartz and Williams, 1972; Schwartz, 1979b). It would be quite interesting to see if the keypeck response topographies produced by water reinforcement in autoshaping and operant situations would more strongly differentiate the effects of the different contingencies underlying these two conditioning paradigms.

In summary, there is little explanatory utility in calling the conditioned response a feeding peck redirected to a signal unless one is simply looking for a shorthand account for the resemblance of the two responses. Since feeding and conditioned responding do not serve the same function and thus do not necessarily share a common causal basis, the explanation of why there are such close similarities in response form remains as much an issue as why there should be differences. Therefore both Jenkins and Moore (1973) and Woodruff and Williams (1976) were right in reporting the resemblance between conditioned and consummatory responses, but wrong with regard to the processes proposed to account for the similarity (Pavlovian elicitation of the unconditioned feeding response through stimulus surrogation;

or, learned-release of a consummatory fixed action pattern). These theoretical viewpoints support a unitary organization for conditioned and consummatory responses and simply beg the question of what factors control the various behavioral elements composing these movement patterns. The results of this study clearly show that there are multiple determinants of response form and that the analysis of the organization of any movement pattern can best be accomplished by examining the control of each of the behavioral elements involved in the response independently. Once the controlling factors for each effector system are known, the organization of these various elements into complex movement patterns can then be more adequately described.

Theoretical assumptions of unitary organization for behavior may partly reflect previous psychological conceptualizations of unitary drives and discrete anatomical "centers" for particular classes of behavior. Traditionally, changes in behavior that were relatively temporary and reversible were considered under the rubric of motivation and were ascribed to changes in the organism's internal state. But the control of behavior can no longer be found in a unitary "cause" termed motivation. At present, usage of the term motivation is somewhat broader in that it concerns the identification of the various factors that may influence behavior and their integration to determine a final behavioral outcome. The motivational process should encompass those factors that initiate, maintain and terminate a particular response. By this view, an important aspect of the study of motivation involves analysis of how an organism produces multiple behavioral outputs from a common effector system by imposing different patterns of muscular contraction. This question requires investigation of the factors controlling response form by dissecting a motor pattern into its smallest behaviorally meaningful units (Barlow, 1968), and then considering a variety of causal factors (both interoceptive and exteroceptive) that are responsible for specific behavioral outcomes.

It is clear that the analysis of any behavior must account for the integration of the direct effects of stimulation upon a substrate of constraints imposed by the internal state of the organism. Psychologists often use the word "context" to refer to the totality of conditions influencing a behavioral event. In the interest of avoiding many of the previous connotations of the term motivation, it might be preferable to use "behavioral context" to refer to the complex of factors influencing an organism's ongoing behavior. Defined in this way, behavioral context could subsume what previously has been considered 'motivational state' and would acknowledge the multiple sources of control that ultimately define those behavior patterns exhibited.

There is no implication that putative causal factors should influence behavior via a single type of mechanism:

Quite often studies that have examined the effects of a single factor in isolation have suffered because of the failure to adknowledge the integration of multiple processes underlying behavior. The various roles of stimuli in the control of movement patterns provides a useful example. Stimuli have been shown to elicit, orient, and pattern movements (Hinde, 1970). Furthermore, stimuli may have physiological consequences determining future responsiveness. Specific cases would be the effects of primer pheromones or certain types of tactile and visual stimulation whose immediate effect is to cause a change in the endocrine state of the receiver that can later produce secondary changes in behavior and responsiveness to stimulation (e.g. Lehrman, 1965). Another example of stimulation having both proximate and long term effects on behavior comes from Kandel's (1976) analysis of the neural basis of behavior in Aplysia. The response of this marine invertebrate to aversive stimulation such as shock includes not only an immediate withdrawal from the point of stimulation, but long term potentiation and inhibition of a variety of behavioral responses mediated by changes in synaptic facilitation and inhibition at specific sites in the nervous system. Bindra's (1971) suggestion that the conditioning process results in response potentiation by facilitation of specific "sensory-motor throughputs" also carries with it the implication that stimuli have both immediate and persistent influences upon behavior.

Such a response potentiation hypothesis may well be consistent with the results of the present study. Clearly the process by which the size of seeds previously eaten influences the determination of beak opening on subsequent pecks must be represented by some relatively persistent change at the neural level. Central potentiation of feeding-related motor outputs may be responsible for many other similarities between consummatory and conditioned responses as well. It is possible that factors such as deprivation state and experience with a particular type of reinforcer have a pervasive influence on response form through central facilitation of certain modes of motor output. This would suggest that features of the consummatory patterns appropriate to deprivation state and reinforcer type are superimposed on conditioned response topography together with the various other factors that have been shown to determine response form. If such a formulation were true, this could lead to a more satisfying account of both the similarities and differences in conditioned and consummatory responses. Ultimately all behavior theory must be reconciled with physiological substrates, and conversely, neurophysiological evidence gains relevance from its implications for behavior. Thus, without further detailed analysis of the form of other conditioned movement patterns (such as water-reinforced key-pecks) and a more adequate knowledge of the neural mechanisms subserving such movements, a full explanation of the control of response form will remain speculation.

Appendix

Technical Note

An Inexpensive Force Transducer for Quantitative Analysis of the Force and Duration of Animal Contact

A force transducing system with associated instrumentation is described for quantitative measurement of the peak force and duration of contact. Figure 16 provides a schematic of the transducer and associated circutry. Outputs are provided for (1) 5 volt logic signals for onset and offset of contact exceeding a threshold force determined by the experimenter, (2) double pole relays operating for the duration of contact, (3) an integrator with an external reset for sampling peak force amplitude and (4) amplifier outputs for continuous monitoring of the analog signal. The force of contact is transduced by a Lafayette Instruments Co. force transducer model #76613. This device consists of a silicon strain gauge attached to a series of stainless steel leaves. Forces applied to the end of the leaves produce limited flexion providing a semi-isotonic transduction with linear output. The force range and displacement can be varied by adjusting the number of steel leaves. The output of the transducer consists of microvolt changes in a baseline voltage produced by variations in the resistance of the strain gauge that serves as an arm of a wheatstone bridge. Transducer excitation voltage is supplied by two twelve-volt batteries. Baseline values can be adjusted by the bridge balance control provided. The low amplitude voltage fluctuations receive amplification that incorporates filtering of all electrical signals above 1000hz. This effectively minimizes atmospheric noise and with appropriate amplifier gain adjustment the amplitude of the voltage change produced by a forceful contact can be increased to about 10 volts. Particular applications will require different combinations of steel leaves in the transducer and gain adjustments. By using three steel leaves of the transducer and a gain of 250, the output of the amplifier was about 1 volt/35 grams of static weight. For applications where a continuous record of contact force over time is required it is useful to display the output of the amplifier on an oscilloscope.

The analog signal is monitored by a solid state voltage comparator that operates the relay and logic pulse outputs. The relationship of the outputs to the analog signal is diagrammed in Figure 17 which shows an oscilloscope waveform produced by a ballistic impact. Determination of a contact force threshold value is accomplished by adjusting the comparator reference voltage. The duration of contact force above the threshold may be timed with either the logic pulses or relay activation. The "B" logic pulse is 8 msec in duration to avoid re-activation by the oscilation that follows rapid, forceful contact. By utilizing solid-state electronics the comparator outputs provide extremely rapid following times useful for activating recording devices with reference to the analog signal (eg. camera strobes, computer sampling devices). An integrator provides a voltage signal proportional to peak force. By "cascading" two integrator circuts with different capacitors the output offers the extremely fast rise time (10 volts/sec) and slow delay (.01 volt/sec) characteristics necessary to catch a single fast peak. The "B" logic pulse (contact offset) can be used to control integrator sampling and reset. Alternatively, sampling with a volt meter and manual reset are possible.

While this force transduction system has many possible applications, the system described here was designed for measurement of the peak force and duration of pigeon key-pecks. In this situation it was desirable to have the capability of rear-projection of stimuli on the surface of the response-key. A diagram of the configuration of the force transducer, floor-mounted response-key and projection system is provided in Figure 18. A Kodak Ectagraphic Projector was mounted below the floor of the experimental chamber 14 inches from the key. The projector was focused on a front-silvered mirror mounted at a 45° angle below the key so that the image was reflected onto the back of the response-surface. The surface material of the response-key was frosted Lucite. The frame by which the key attached to the transducer was constructed of .125 inch aluminum tubing and brass stock glued with Epoxy. It is important to keep the sprung-weight of the response-key as low as possible for optimum response characteristics and for this reason the mirror was mounted independently of the response key.

INDEPENDENT VARIABLES

- EATING SITUATIONS
  - SEED SIZE (3-5mm, 6-8mm, 10-12mm)
- CONDITIONING SITUATIONS
  - CONTINGENCY
    - PAVLOVIAN (AUTOSHAPING)
    - OPERANT (CRF, VR3, EXTINCTION)
  - SIGNAL PROPERTIES
    - BLACK DOTS (SIGNALS WITH TARGETS, 5 SIZES)
    - WHITE DOTS (SIGNALS AS TARGETS, 5 SIZES)
    - SEED ON KEY
  - REINFORCER
    - SEED SIZE (MILO 3-5mm, PEA 6-8mm)

DEPENDENT VARIABLES

- FORCE
- DURATION
- BEAK OPENING (GAPE)
- EYE CLOSURE
- PECK LOCATION WITH RESPECT TO TARGETS

Table I

Table II. Training schedule for Autoshaping and Operant Conditioning groups.

Autoshaping

Signal	Reinforcer	Sessions/Responses
plain	milo	100 responses
black-dots	milo	1 session
white-dots	milo	1 session
plain	pea	2 sessions
seed key	milo	1 session
eating	3 seed sizes	25 responses for each seed size

Operant

Signal	Reinforcer	Schedule	Sessions/Responses
plain	milo	CRF	100 responses
plain	milo	VR3	100 responses
black-dots	milo	VR3	1 session
white-dots	milo	VR3	1 session
plain	pea	VR3	2 sessions
seed key	milo	VR3	1 session
plain	milo	Extinction	1 session
eating	3 seed sizes	----	25 responses for each seed size

Table III. Statistical comparison of feeding and conditioned response contact force. Means and standard deviations (mean/std.dev.) are given in grams.

Autoshaping

Subject	237	247	249	282	812	Combined
autoshaping	64.6/ 25.5	51.8/ 20.2	137.9/ 37.4	79.1/ 26.2	109.1/ 47.6	88.5/ 34.9
eating	43.4/ 27.3	50.4/ 29.0	20.6/ 15.7	50.0/ 35.0	57.0/ 33.6	44.3/ 13.9
p value** (one-tailed)	.0002	.72*	.0001	.0001	.0001	.0001

Operant

Subject	251	255	262	281	774	Combined
operant	51.8/ 19.6	71.7/ 28.7	116.9/ 51.8	76.6/ 24.9	64.7/ 25.2	76.3/ 24.5
eating	47.6/ 26.9	35.3/ 19.9	35.0/ 21.7	29.5/ 17.4	43.4/ 22.7	38.2/ 7.2
p value** (one-tailed)	.37*	.0001	.0001	.0001	.0001	.0001

* Not significant

**Individual t-statistics were calculated with degrees of freedom adjusted according to Welch's solution to the Behrens-Fisher problem (Wang, 1971). All tests in each group were combined using the Fisher Method (Fisher, 1942).

Table IV. Statistical Comparison of response form with operant CRF and VR3 Schedules. Means and Standard deviations (mean/std.dev) are given for each subject.

Subject	251	255	262	281	774	Group Mean
FORCE (grams)						
CRF	1.67/ .43	1.98/ 1.12	2.43/ .88	2.74/ .74	1.79/ .52	2.12
VR3	1.49/ .56	2.05/ .82	3.34/ 1.48	2.19/ .71	1.85/ .72	2.18
P Value**	.0009	.61*	.0001	.0001	.39	
DURATION (msec.)						
CRF	8.59/ 2.37	9.68/ 2.94	9.13/ 2.15	11.14/ 1.73	8.01/ 2.79	9.31
VR3	7.25/ 2.23	8.88/ 2.93	10.53/ 4.46	9.84/ 2.03	8.32/ 3.92	8.96
P Value**	.0001	.072*	.008	.0001	.43*	
GAPE (mm.)						
CRF	4.16/ 1.33	6.36/ 1.58	4.82. 1.58	7.84/ 1.09	3.59/ 1.59	5.35
VR3	5.35/ 2.24	6.21/ 1.86	5.17/ 1.94	7.44/ 1.23	4.29/ 1.59	5.69
P Value*	.0001	.56*	.19*	.009	.0007	
EYE (mm.)						
CRF	2.99/ 1.08	1.89/ 0.80	0.83/ 0.59	2.36/ 0.65	0.76/ 0.71	1.76
VR3	2.87/ 1.24	1.49/ 0.74	0.79/ 0.49	2.49/ 0.73	0.79/ 0.43	1.69
P Value**	.32*	.0006	.61*	.15*	.74*	

* not significant

** Individual t-statistics were calculated with degrees of freedom adjusted according to Welch's solution to the Behrens-Fisher problem (Wang, 1971).

Table V. Statistical Comparison of keypeck force with operant VR3 and extinction schedules. Means and Standard deviations (mean/std.dev) are given in grams for each subject.

Subject	251	255	262	281	774
operant VR3	52.0/ 19.6	1.85/ 28.7	116.93/ 51.9	76.89/ 24.8	64.7/ 25.2
extinction	68.1/ 23.3	134.0/ 51.3	103.9/ 44.4	90.54/ 23.8	78.0/ 29.3
P-value**	.0003	.0001	.26*	.0001	.002

* not significant

** individual t-statistics were calculated with degrees of freedom adjusted according to Welch's solution to the Behrens-Fisher problem (Wang, 1971).

Table VI . Mean gape in millimeters for individual subjects with milo and pea reinforcement.

Autoshaping

Subject	237	247	282	812	Combined
milo	3.1	3.1	7.9	5.2	4.8
pea	5.0	3.2	9.3	6.6	6.0
p value**	.0001	.68*	.0001	.0001	.0001

Operant

Subject	251	255	262	281	774	Combined
milo	5.3	6.2	5.2	7.4	4.3	5.7
pea	9.2	9.7	7.3	9.3	7.6	8.6
p value**	.0001	.0001	.0001	.0001	.0001	.0001

* Not significant.

** Individual t-statistics were calculated with degrees of freedom adjusted according to Welch's solution to the Behrens-Fisher problem (Wang, 1971). All tests in each group were combined using the Fisher Method (Fisher, 1942).

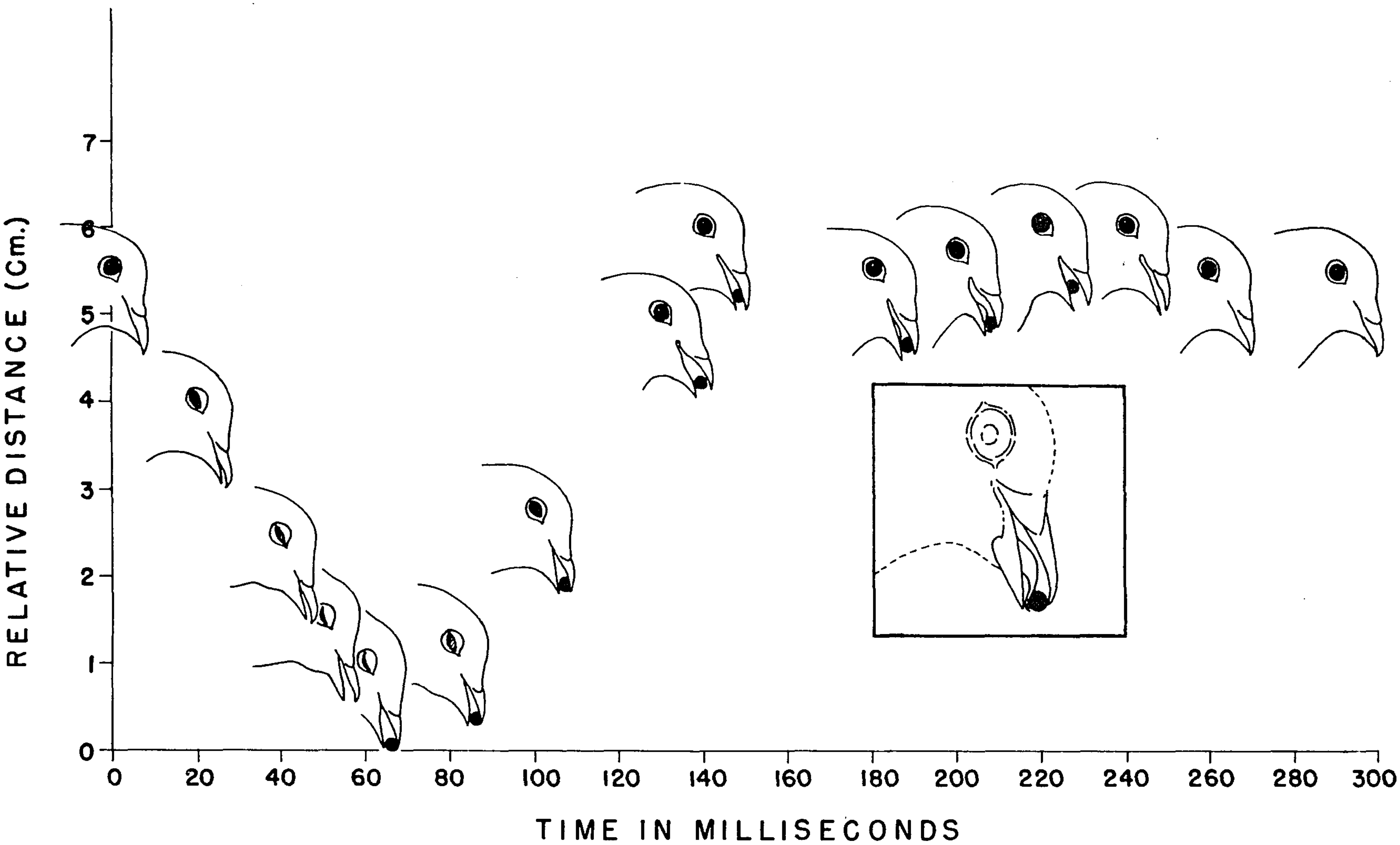

RELATIVE DISTANCE (Cm.)
7
6
5
4
3
2
1
0
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
TIME IN MILLISECONDS

Figure 1.

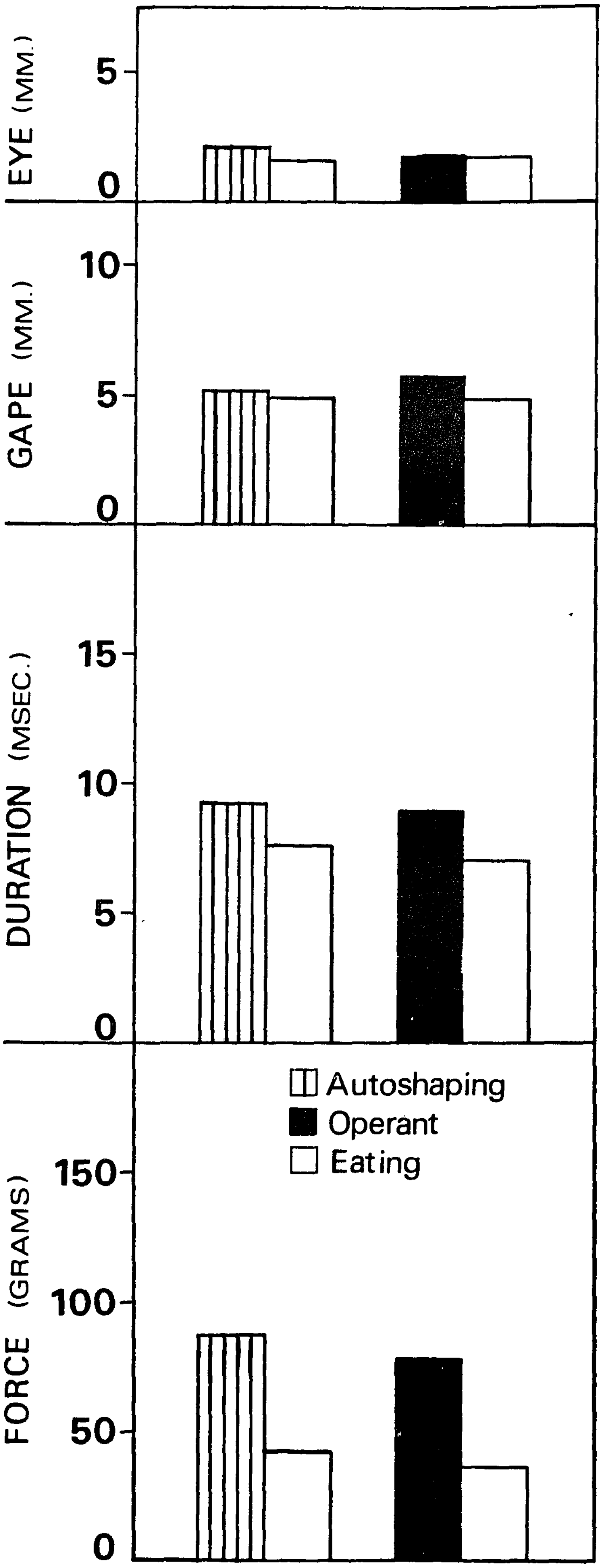
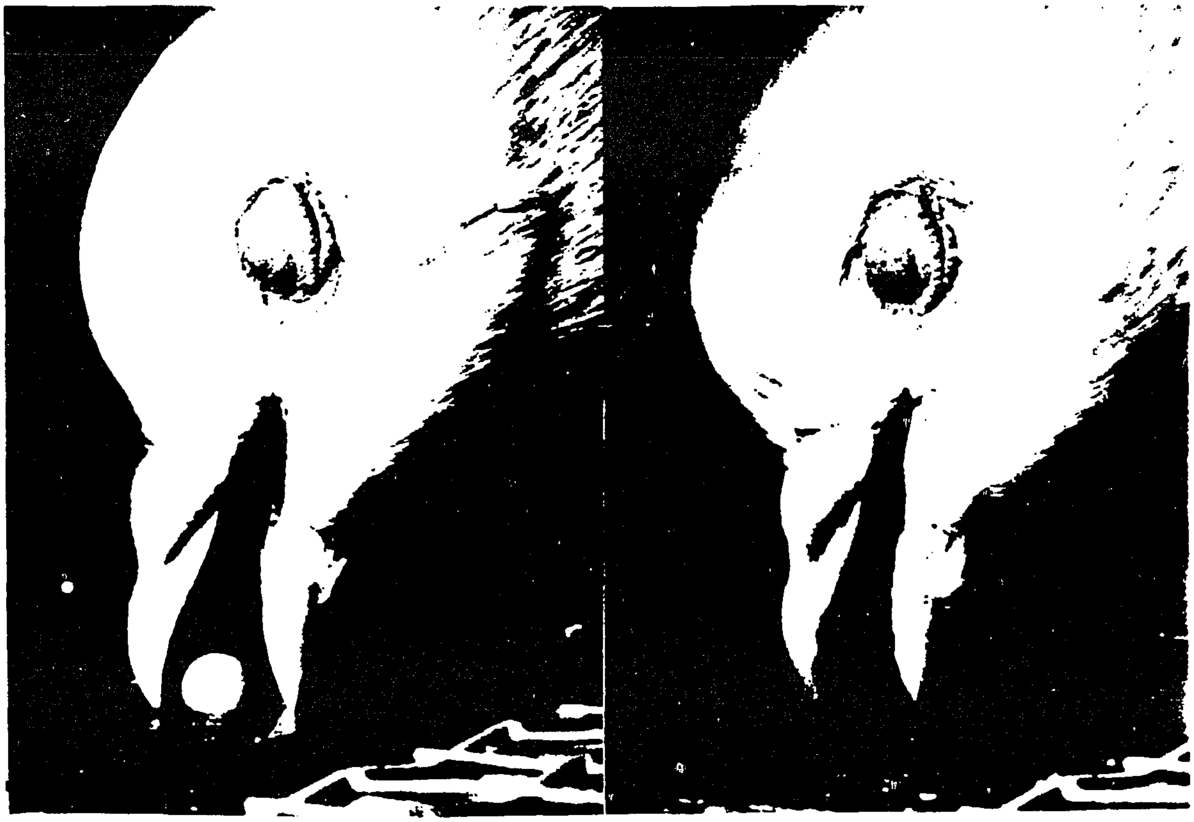

EYE (MM.)
5
0
GAPE (MM.)
10
5
0
DURATION (MSEC.)
15
10
5
0
FORCE (GRAMS)
150
100
50
0
Autoshaping
Operant
Eating

Figure 2.



FEEDING CONDITIONED KEYPECK

Figure 3. Photographs show typical feeding and conditioned responses recorded in the experiments. Note for feeding response beak is open slightly greater than seed diameter and that for both responses the eye is nearly closed.

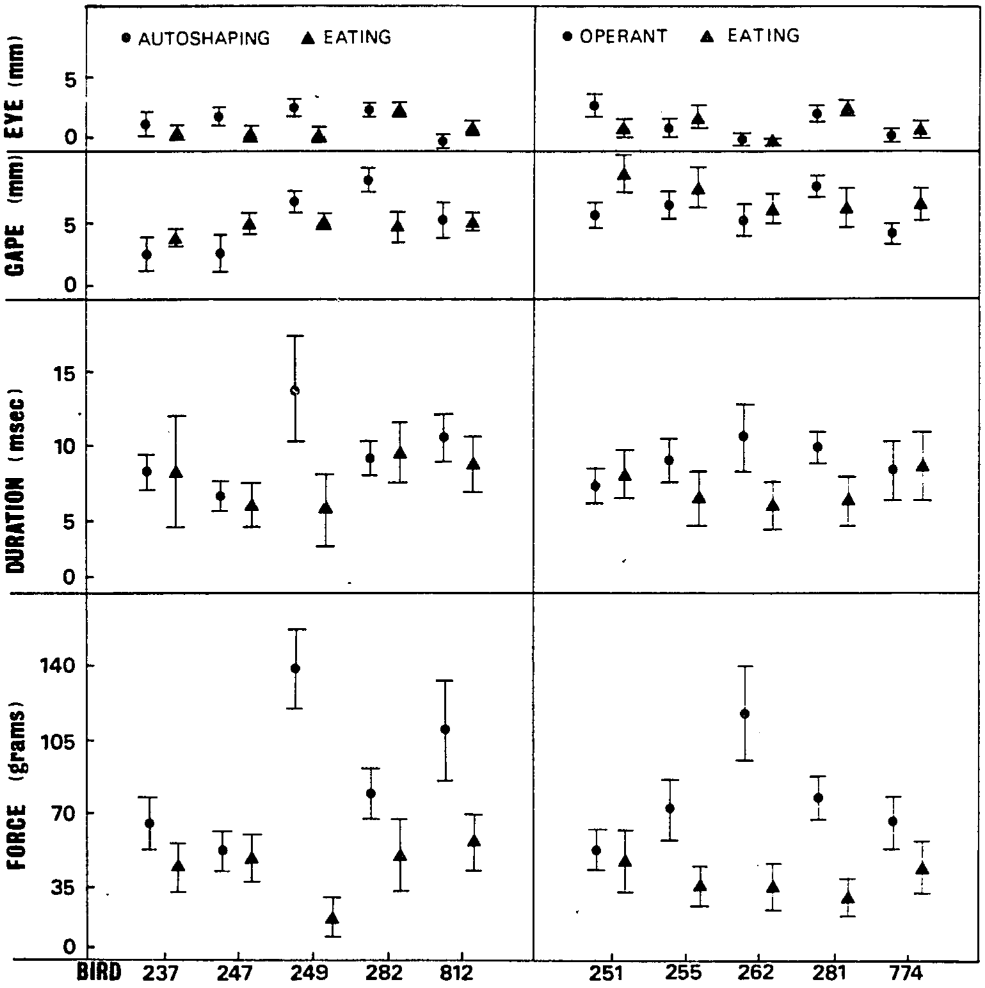
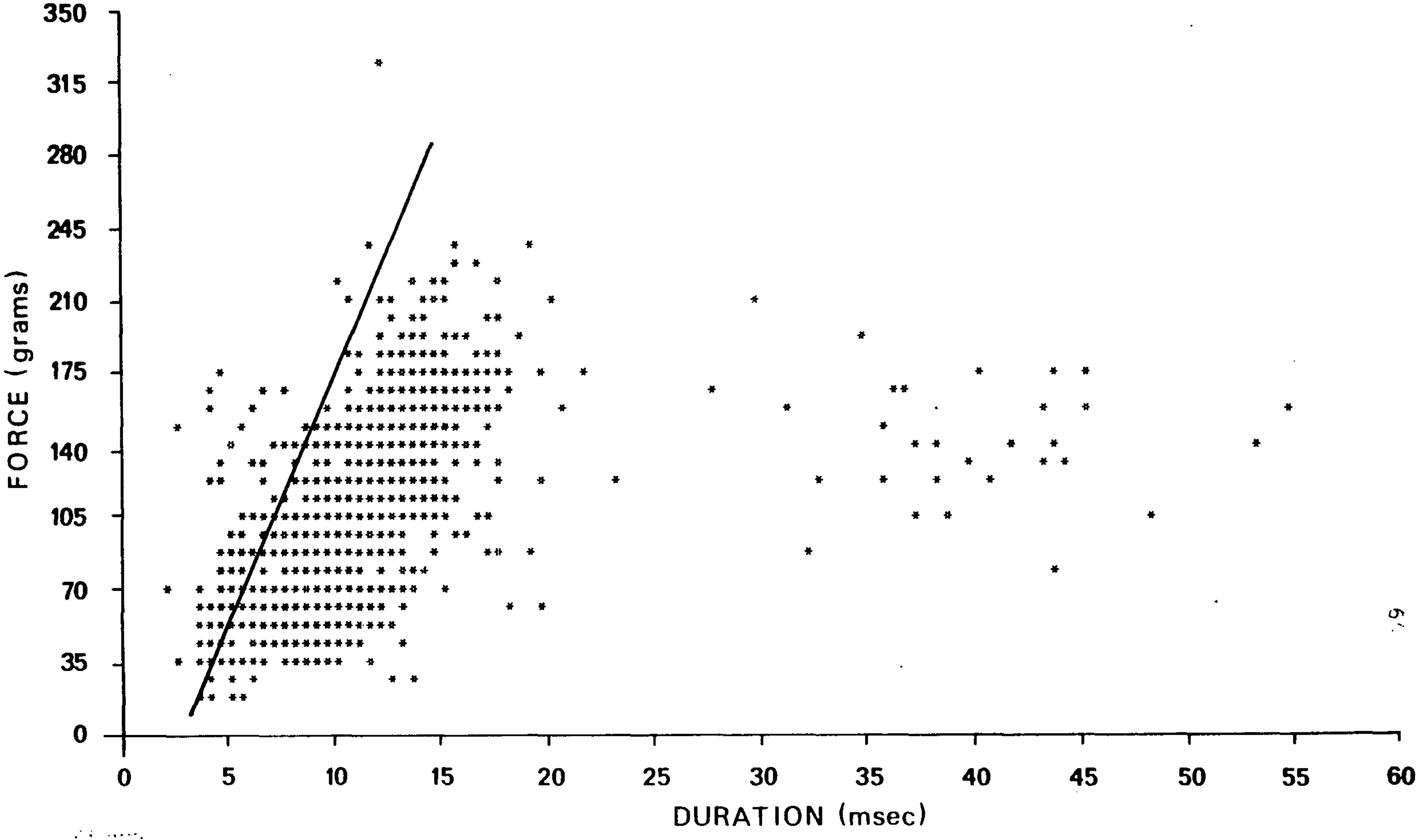

● AUTOSHAPING ▲ EATING
● OPERANT ▲ EATING
EYE (mm)
5
0
GAPE (mm)
5
0
DURATION (msec)
15
10
5
0
FORCE (grams)
140
105
70
35
0
BIRD
237
247
249
282
812
251
255
262
281
774

Figure [illegible]


FORCE (grams)
350
315
280
245
210
175
140
105
70
35
0
0
5
10
15
20
25
30
35
40
45
50
55
60
DURATION (msec)

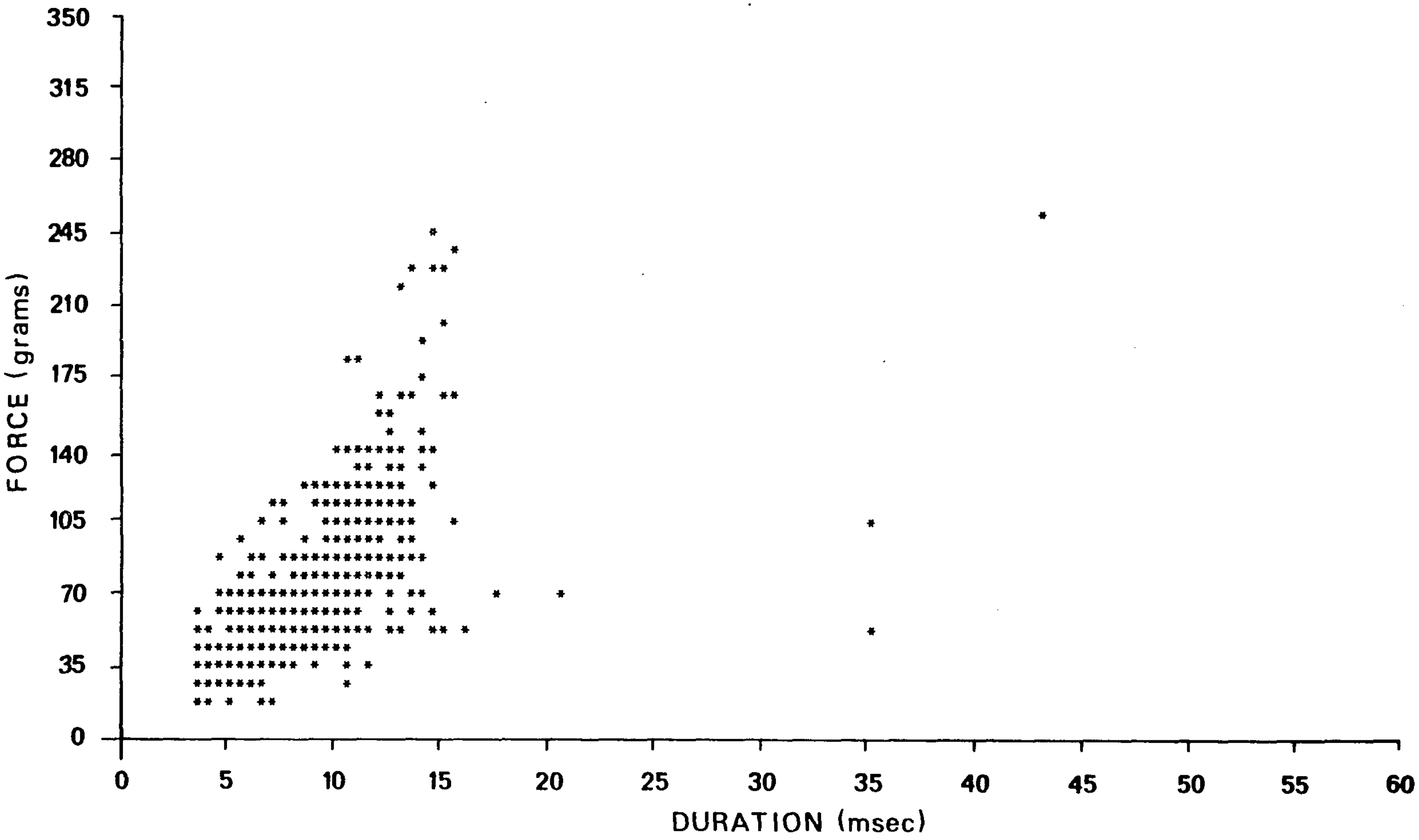

FORCE (grams)
350
315
280
245
210
175
140
105
70
35
0
0
5
10
15
20
25
30
35
40
45
50
55
60
DURATION (msec)

Figure 6.

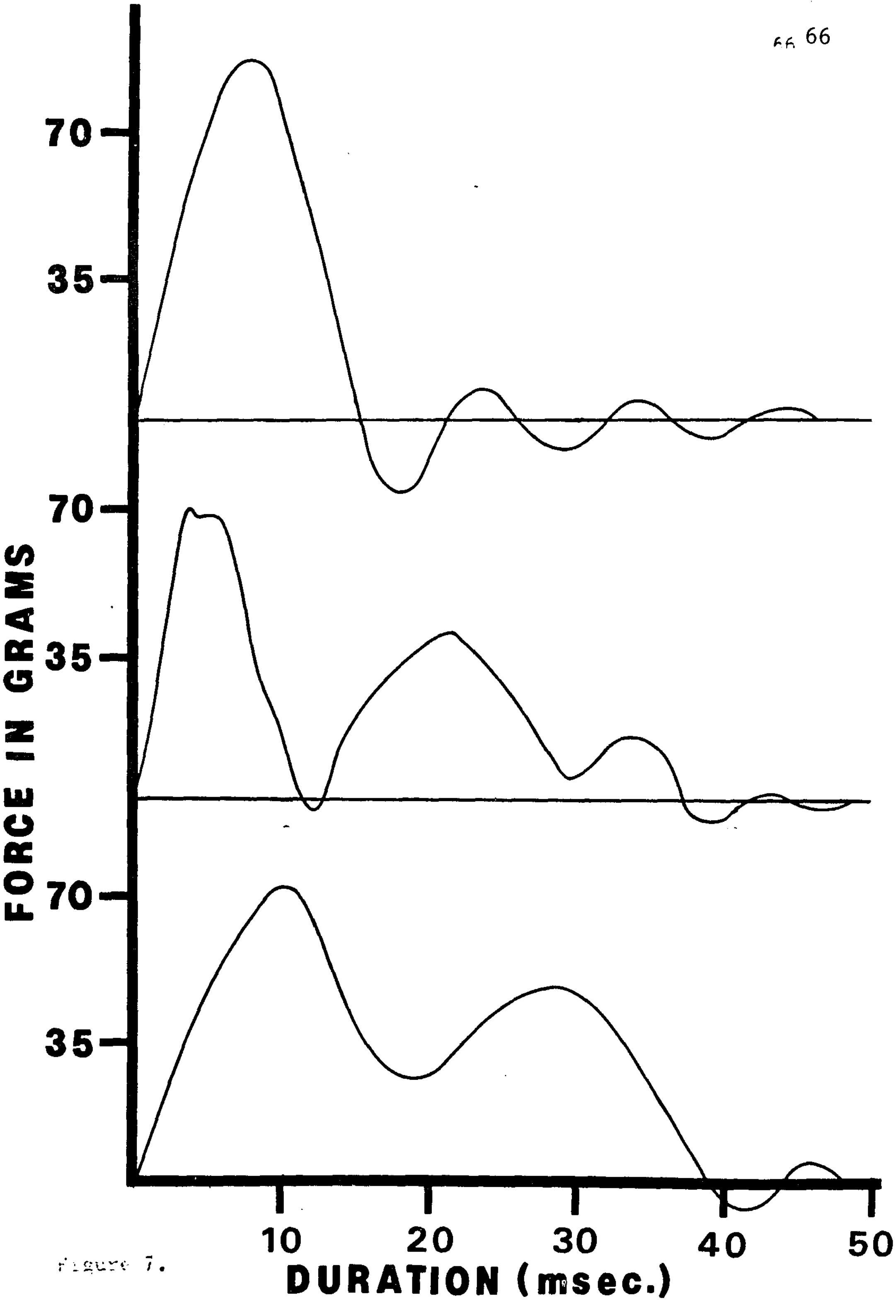
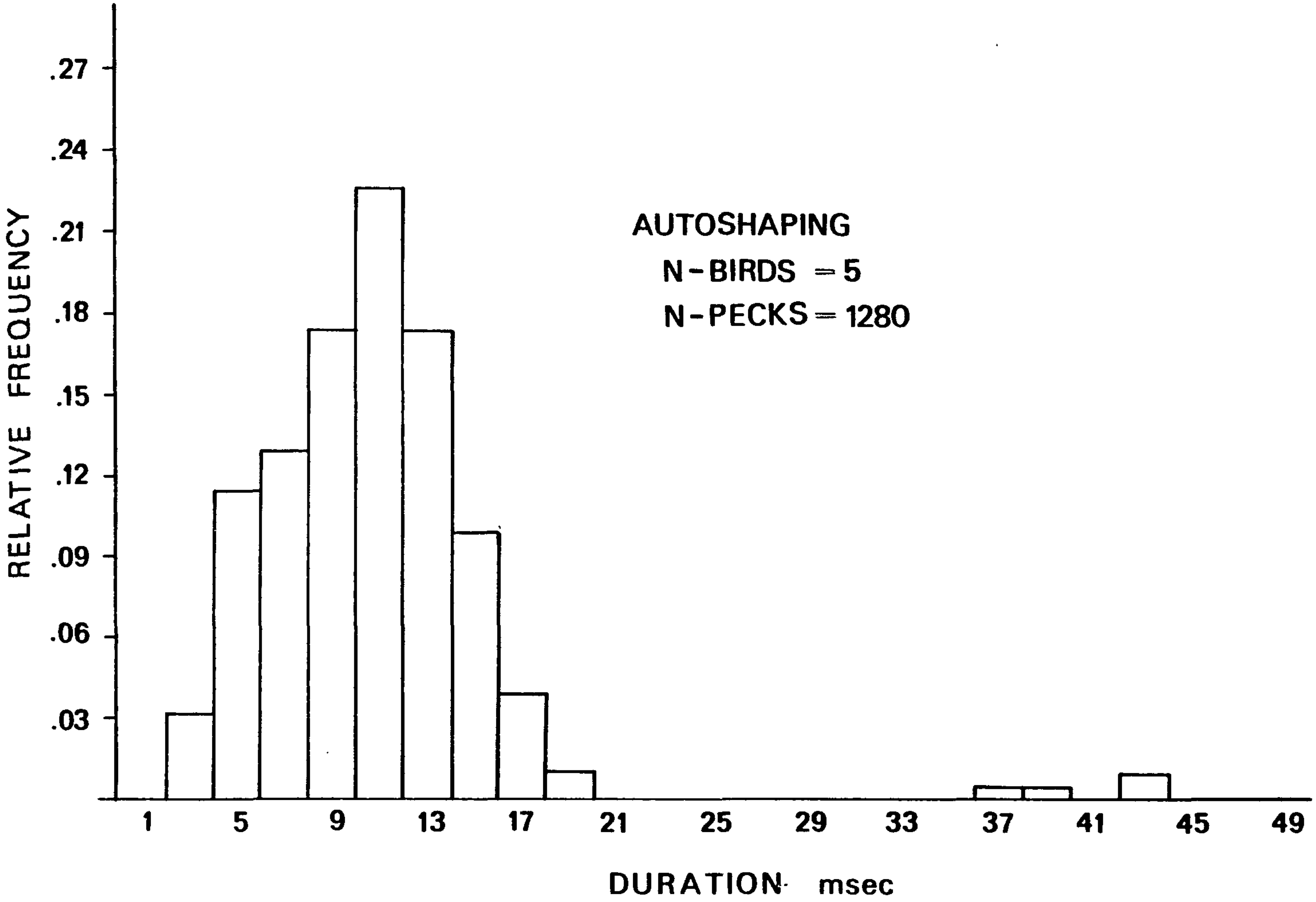


Figure 7.



AUTOSHAPING
N-BIRDS = 5
N-PECKS = 1280
RELATIVE FREQUENCY
.27
.24
.21
.18
.15
.12
.09
.06
.03
1
5
9
13
17
21
25
29
33
37
41
45
49
DURATION msec

Figure 8.

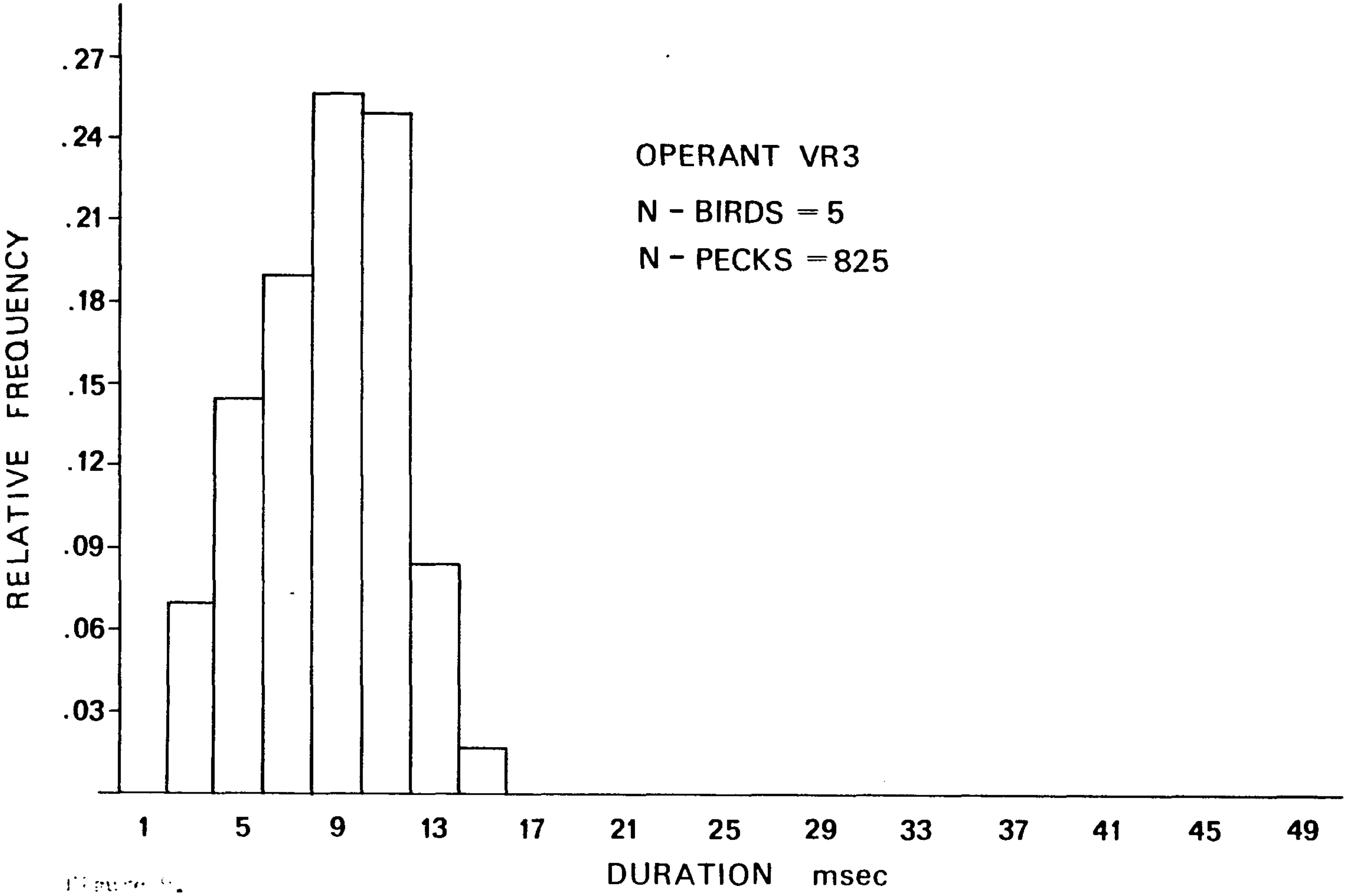

OPERANT VR3
N - BIRDS = 5
N - PECKS = 825
RELATIVE FREQUENCY
.27
.24
.21
.18
.15
.12
.09
.06
.03
1
5
9
13
17
21
25
29
33
37
41
45
49
DURATION msec

Figure [illegible].

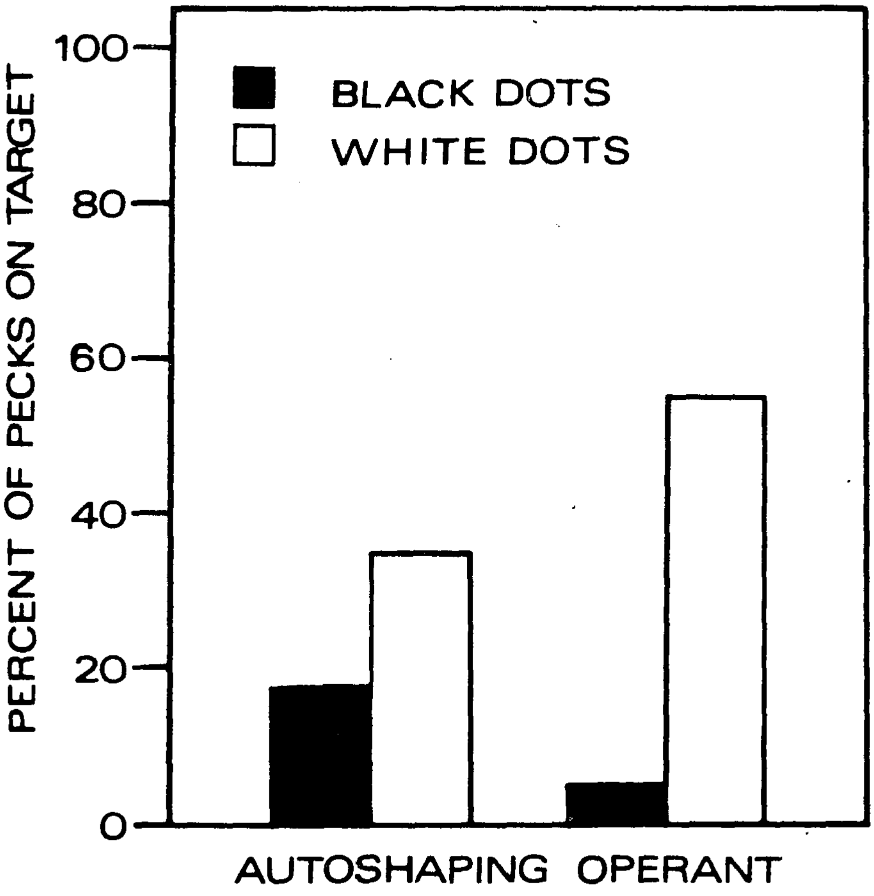

100
80
60
40
20
0
PERCENT OF PECKS ON TARGET
■ BLACK DOTS
□ WHITE DOTS
AUTOSHAPING
OPERANT

Figure 10.

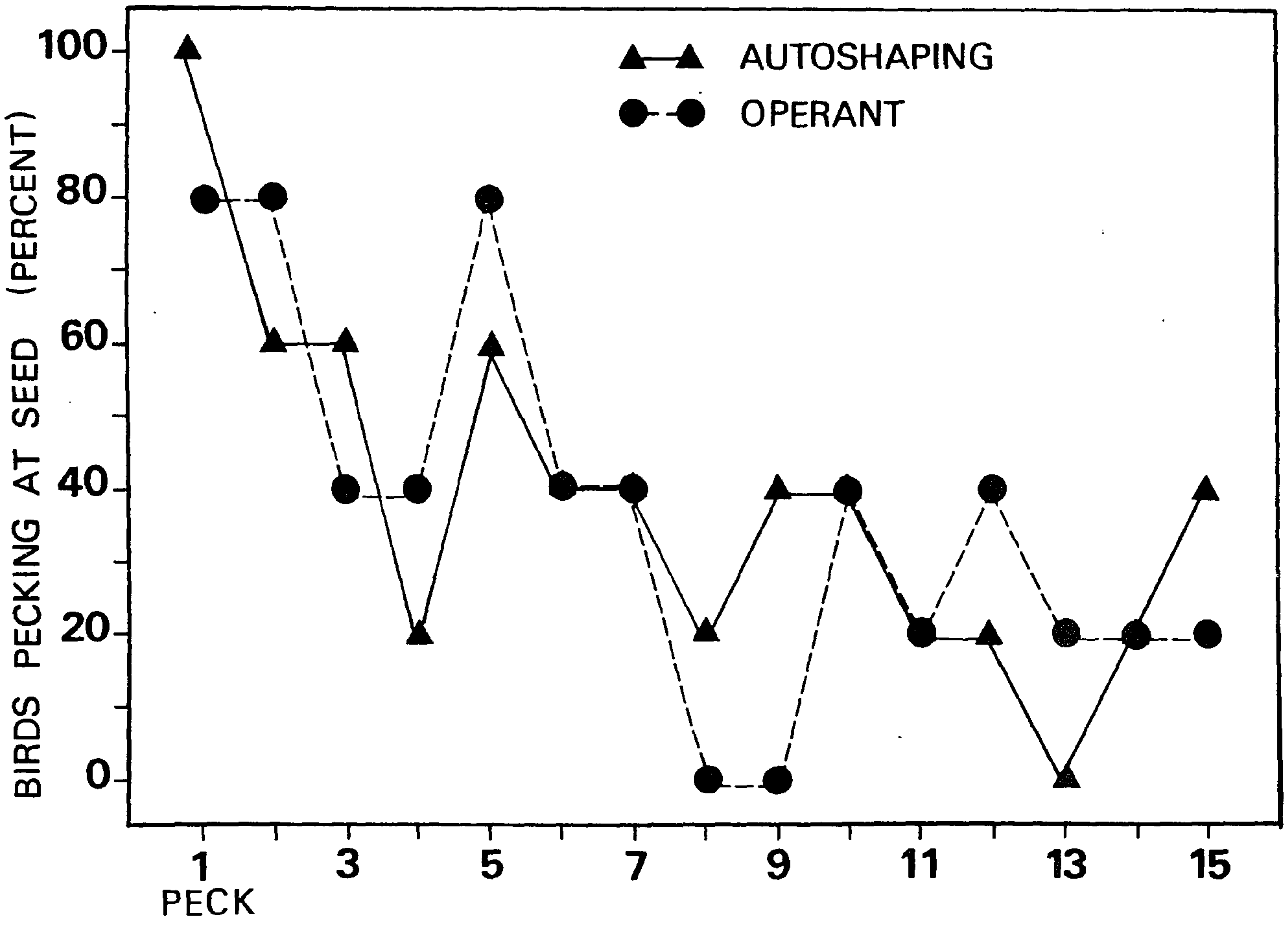

AUTOSHAPING
OPERANT
BIRDS PECKING AT SEED (PERCENT)
100
80
60
40
20
0
1
3
5
7
9
11
13
15
PECK

Figure 11.

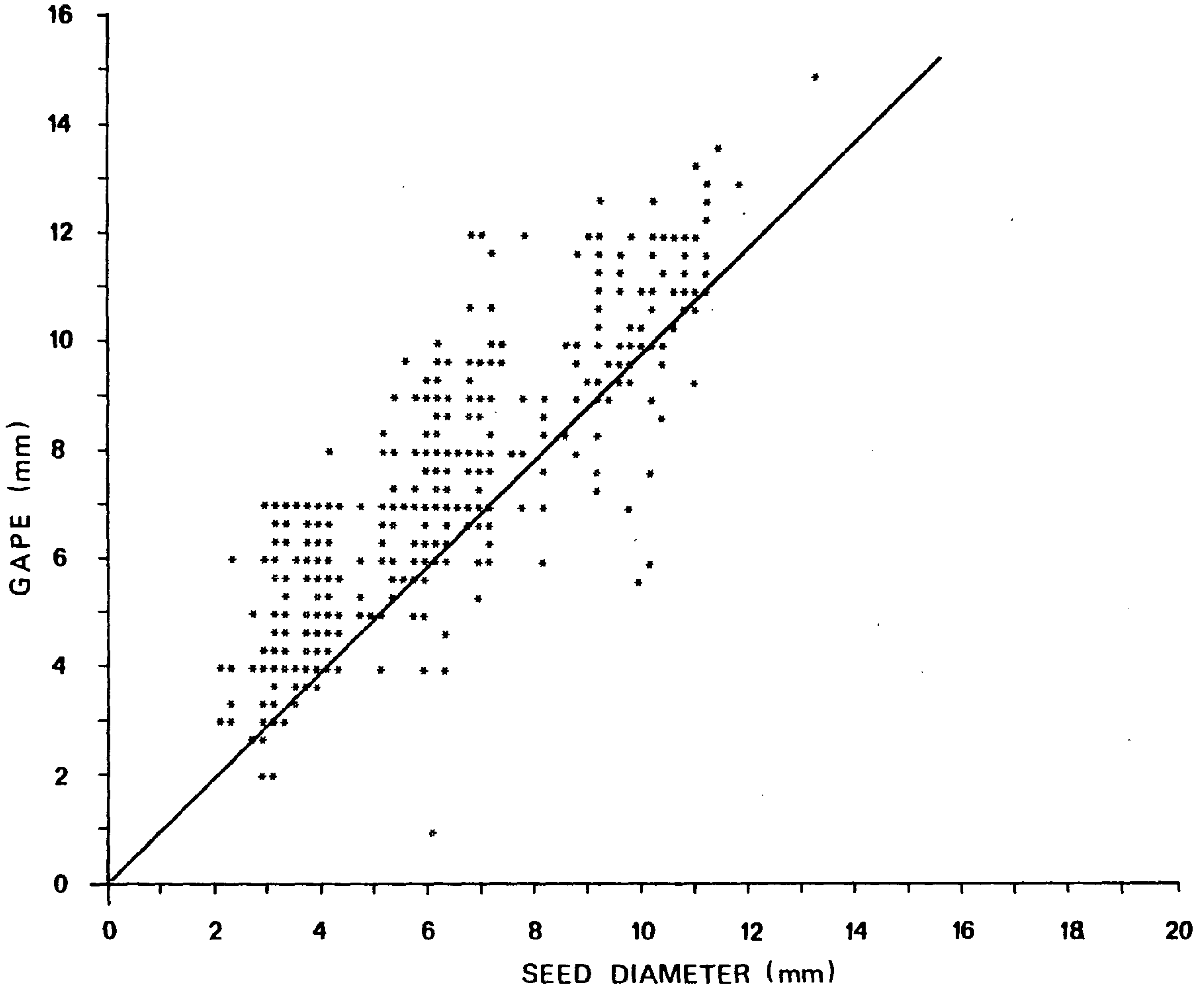
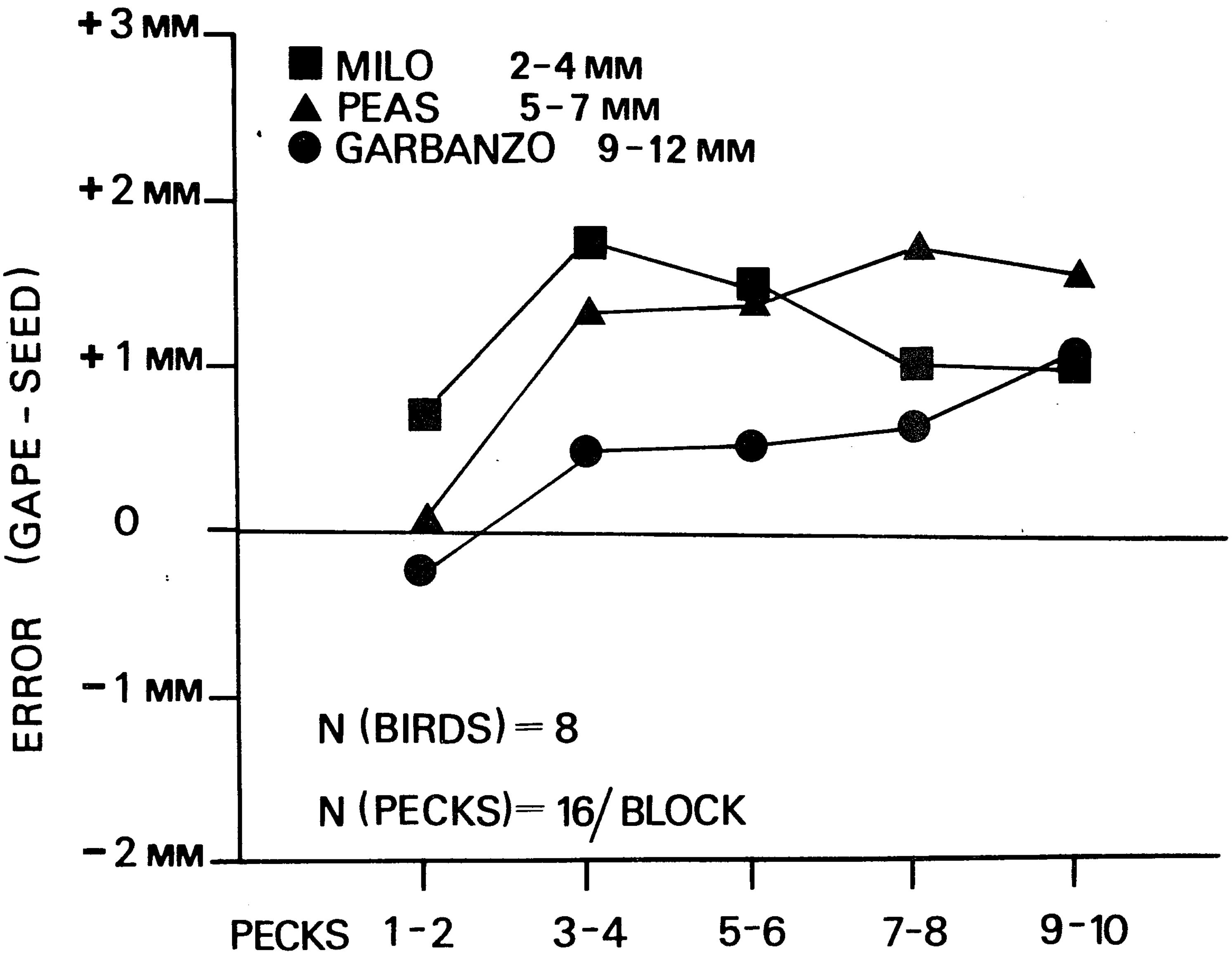

GAPE (mm)
0
2
4
6
8
10
12
14
16
SEED DIAMETER (mm)
0
2
4
6
8
10
12
14
16
18
20

Figure [illegible]



+3 MM
+2 MM
+1 MM
0
−1 MM
−2 MM
ERROR (GAPE - SEED)
■ MILO 2-4 MM
▲ PEAS 5-7 MM
● GARBANZO 9-12 MM
N (BIRDS) = 8
N (PECKS) = 16/ BLOCK
PECKS
1-2
3-4
5-6
7-8
9-10

Figure 13.

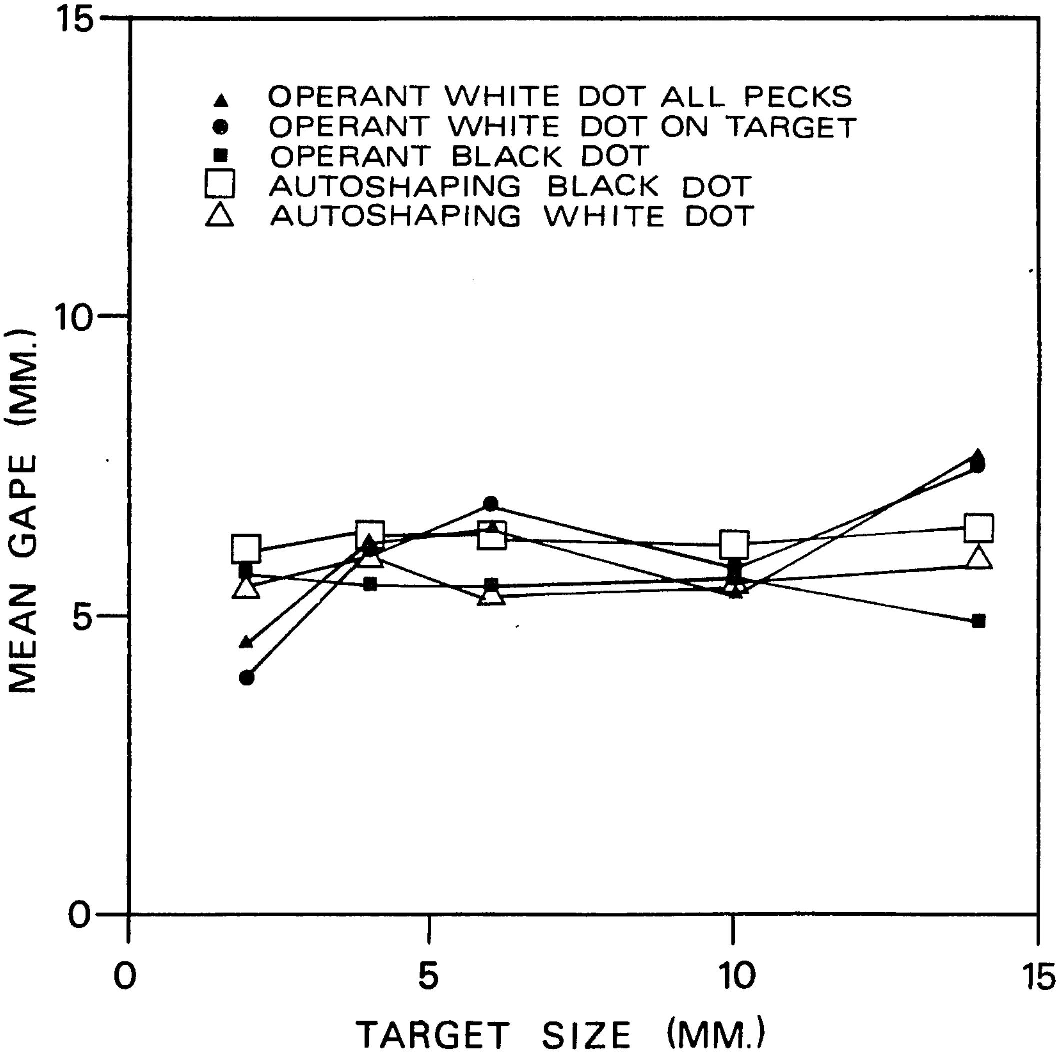

▲ OPERANT WHITE DOT ALL PECKS
● OPERANT WHITE DOT ON TARGET
■ OPERANT BLACK DOT
□ AUTOSHAPING BLACK DOT
△ AUTOSHAPING WHITE DOT
15
10
5
0
MEAN GAPE (MM.)
0
5
10
15
TARGET SIZE (MM.)

Figure 14.

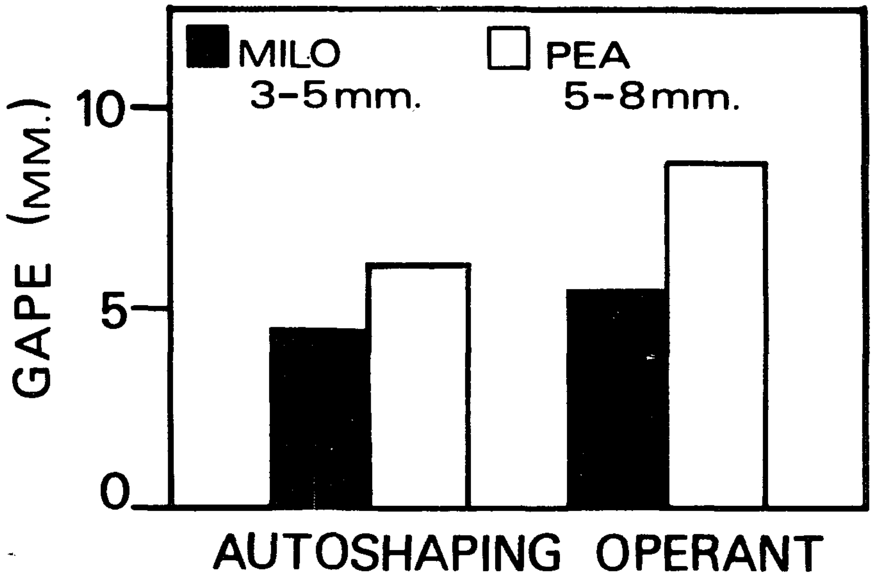


Figure 15.

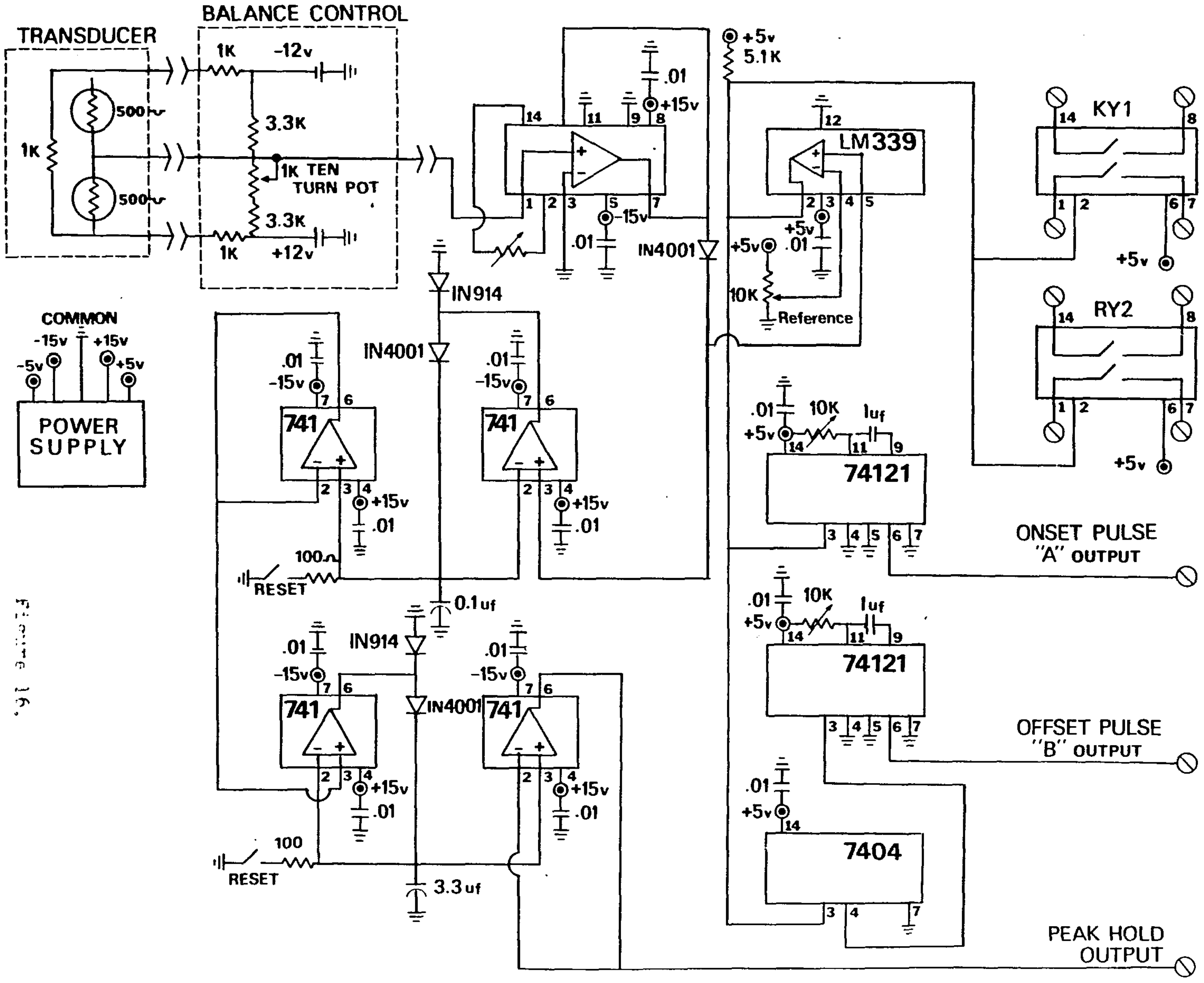
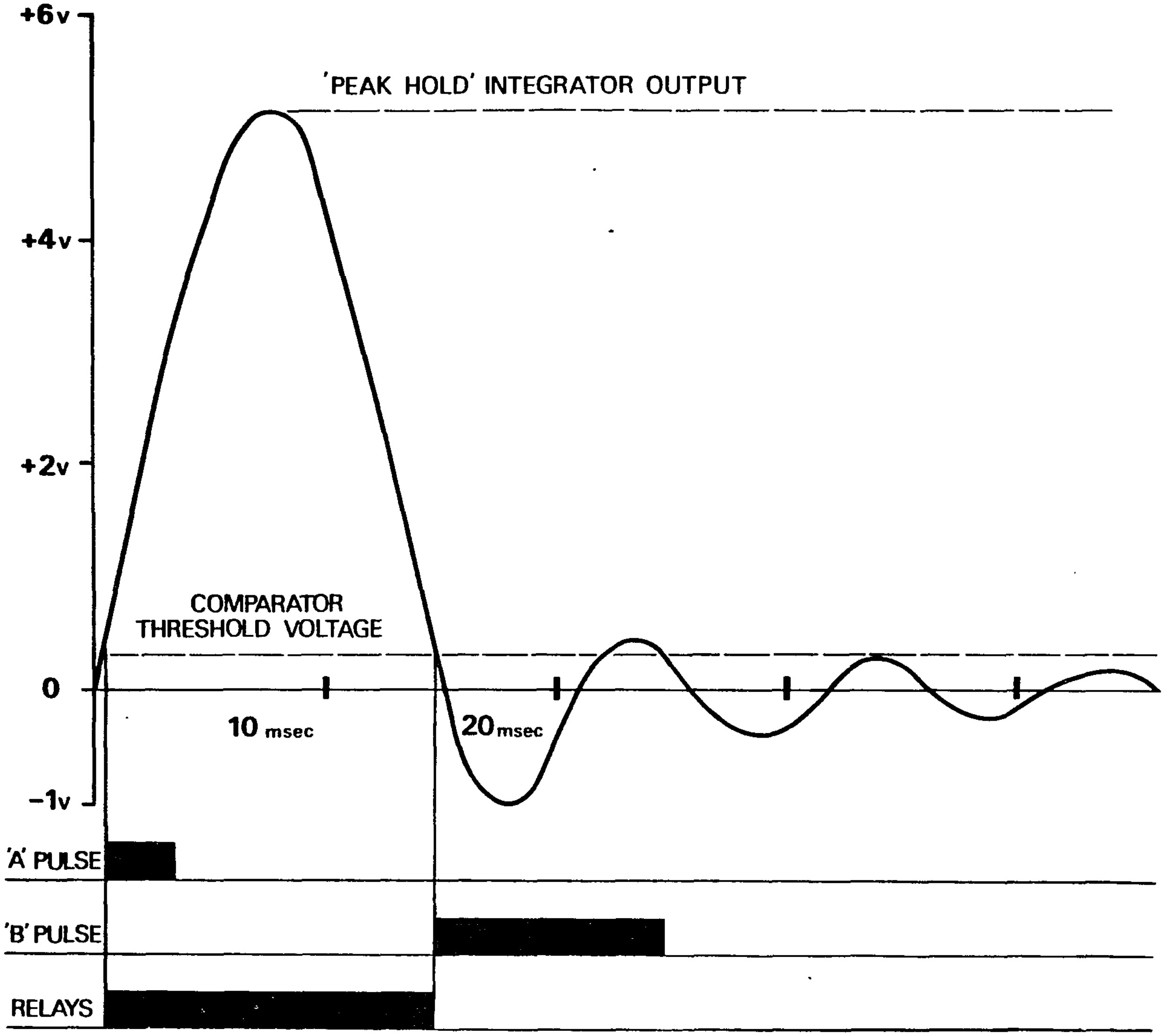

TRANSDUCER
BALANCE CONTROL
1K
500~
500~
1K
-12v
3.3K
1K TEN TURN POT
3.3K
1K
+12v
14
11
9
8
.01
+15v
1
2
3
5
-15v
7
.01
IN4001
+5v
5.1K
12
LM339
2
3
4
5
+5v
.01
+5v
10K
Reference
KY1
14
8
1
2
6
7
+5v
RY2
14
8
1
2
6
7
+5v
COMMON
-15v
+15v
-5v
+5v
POWER SUPPLY
IN914
IN4001
.01
-15v
7
6
741
2
3
4
+15v
.01
.01
-15v
7
6
741
2
3
4
+15v
.01
100
RESET
0.1uf
IN914
IN4001
.01
-15v
7
6
741
2
3
4
+15v
.01
.01
-15v
7
6
741
2
3
4
+15v
.01
100
RESET
3.3uf
.01
10K
1uf
+5v
14
11
9
74121
3
4
5
6
7
ONSET PULSE "A" OUTPUT
.01
10K
1uf
+5v
14
11
9
74121
3
4
5
6
7
OFFSET PULSE "B" OUTPUT
.01
+5v
14
7404
3
4
7
PEAK HOLD OUTPUT

Figure 16.


+6v
'PEAK HOLD' INTEGRATOR OUTPUT
+4v
+2v
COMPARATOR
THRESHOLD VOLTAGE
0
10 msec
20 msec
-1v
'A' PULSE
'B' PULSE
RELAYS

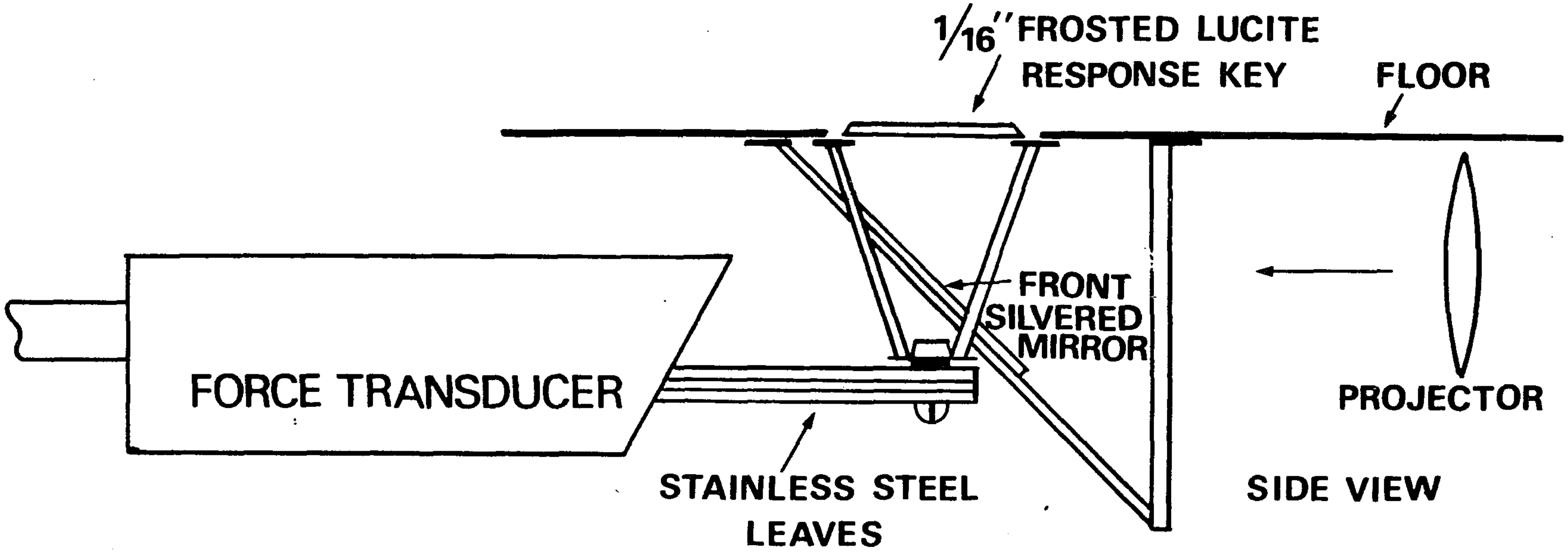

1/16" FROSTED LUCITE
RESPONSE KEY
FLOOR
FRONT
SILVERED
MIRROR
FORCE TRANSDUCER
PROJECTOR
STAINLESS STEEL
LEAVES
SIDE VIEW

Figure 18.

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