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DESCRIPTIVE AND KINEMATIC ANALYSIS OF JAW MOVEMENTS DURING EATING BEHAVIOR IN THE PIGEON

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DESCRIPTIVE AND KINEMATIC ANALYSIS OF JAW MOVEMENTS DURING EATING BEHAVIOR IN THE PIGEON

by

ROBERTO BERMEJO

A dissertation submitted to the Graduate Faculty in Psychology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1987

This manuscript has been read and accepted for the Graduate Faculty in Psychology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

DESCRIPTIVE AND KINEMATIC ANALYSIS OF JAW MOVEMENTS DURING EATING BEHAVIOR IN THE PIGEON

by

Roberto Bermejo

Adviser: Professor H. Philip Zeigler

Eating behavior in the pigeon involves relatively stereotyped and naturally occurring movement patterns which are generated by a simple effector organ, the jaw.

The present study was designed to:

1) Characterize the different movement types during the eating sequence.

2) Provide an analysis of the kinematics of these movement classes.

Jaw opening movements during pecking at targets (food pellets) of six different sizes were recorded "on-line" using a transducing system generating a voltage output proportional to gape (interbeak distance). Jaw opening amplitude and its first and second derivatives (velocity, acceleration), were measured for each gape as was rise time to peak amplitude. Correlations between target size and each of the kinematic variables were calculated as were correlations among the kinematic variables.

For some of the movement types, the peak velocity and peak acceleration of the jaw opening response are scaled to target size and highly predictive of its peak amplitude, suggesting that critical parameters of the response have been programmed prior to response initiation. Correlations with rise time, though significant, are considerably smaller. Multiple regression analysis of the data suggest that:

1) For both grasp and mandibulation, a pulse-height model accounts for most of the variance in the opening amplitude.

2) For grasping, but not for mandibulation, rise time contributes to the control of the amplitude by correcting the deviations (errors) in the initial programmed trajectory.

3) Rise time during mandibulation movements are significantly faster than during grasping, and are inversely proportional to the target size.

The motor control strategy used by the pigeon in its grasping behavior is similar to that used by cats and humans to control the scaling of isometric force in tasks involving limb muscles. Given the simplicity of the jaw as an effector system, the pigeon's grasping behavior may be a useful model system for the study of neural mechanisms of motor control.

ACKNOWLEDGEMENTS

Although a Ph.D. thesis is submitted by a single person, who gets all the credit by achieving a doctoral degree, it really represents the work of a team. Within this team, the graduate student grows until he/she reaches the required levels of expertise and good skills, as well as self-confidence. In this way, I would like to express my gratitude to those who have contributed to make me feel and think as a scientist.

Dr. H. Philip Zeigler, my mentor and teacher. His expertise was a constant source of confidence, and his daily work reflected the security that even the hardest experiments would succeed easily. His enthusiasm to solve problems, and his continuous thinking on how to deal with them, keeps his laboratory alive and full of youthful energy. There are no words to appreciate his constant supervision and help, without which this work would not have been yet finished.

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Dr. Peter Moller, member of my thesis committee and teacher. I learned from him that the more we integrate biology and behavior the better psychology can explain the phenomenon of behavior.

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GENERAL INTRODUCTION

The study of neural mechanisms of motor control has focused on species-typical behaviors in vertebrates and invertebrates as well as on complex, learned motor tasks in primates. The invertebrate preparations usually involve fixed action patterns which, while relatively simple, may be of limited generality for vertebrates (Bullock, 1986; Mountcastle, 1986). Examples of vertebrate studies iclude locomotion in the lamprey (Grillner, Wallen, McClellan, Sigvardt, Williams, and Feldman, 1983); prey-catching behavior in the toad (Ewert, 1980; Satuo, Matsushina, Takeuchi and Ueda, 1985) and the scratch reflex in the spinal turtle (Stein, 1983). The primate behaviors are either extremely complex or artificially constrained to such an extent that their generalization to normal voluntary motor behavior may be questioned (Polit and Bizzi, 1979). For these reasons it may be useful to study motor control mechanisms in a vertebrate species whose behavior can functionally approximate that of primates but involves relatively stereotyped, species-typical movement patterns which are generated by a simple effector system. The pigeon's eating behavior can provide an intermediate preparation for such studies. This behavior has several characteristics that makes it very useful for the study of motor control (Bermejo and Zeigler, 1986):

1) Pigeons posses a well developed visual system (Emmerton, 1983) and a prehensile effector organ (the beak),

which is richly supplied with mechanoreceptors (Berkhoudt, 1980; Necker, 1983), and under precise motor control (Bock, 1964). The pigeon's beak participates in a wide variety of species-typical behaviors involving eating (including grasping and manipulation), grooming, agonistic behavior, and parental care.

2) LaMon and Zeigler (1984) have shown that grasping in the pigeon involves an adjustment of the effector organ to the size of the target which is completed prior to contact. Jaw opening (gape) prior to grasping is linearly related to the size of the seed over a wide range of target sizes.

3) Grasping is mediated by a relatively simple effector organ, the jaw, involving only seven muscles, five closers and two openers (Wild and Zeigler, 1980).

4) The components of a neural circuit connecting jaw mechanoreceptors to jaw motoneurons have been identified (Berkhoudt, Klein and Zeigler, 1982; Wild, Arends and Zeigler, 1984, 1985), providing an opportunity to study the neural basis of the behavior.

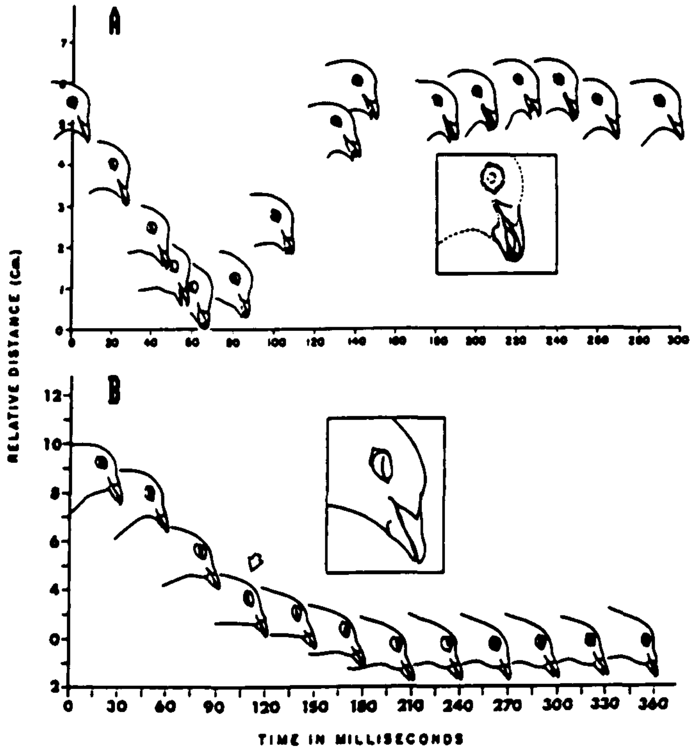
Pecking/grasping as a motor problem

Pecking behavior during eating may be subdivided into four distinct phases: Pecking, grasping, mandibulation, and swallowing (Figure 1, from Zeigler, Levitt and Levine, 1980):

1) **Pecking** is preceded by one or more fixations, lasting at least 100 ms., during which the head is kept in position above the seed at distances between 30-100 mm. It in-

volves a downward movement of the head elicited by and directed toward a stimulus target.

2) **Grasping** is integrated into the pecking response and may be further subdivided into opening and closing phases. At the start of the peck, the eye is open and beak aperture begins 25-30 ms afterwards. The peck concludes with the eyes almost shut and the beak open around the seed. The closing phase normally terminates with the seed grasped between the beak tips. The entire grasping sequence takes about 60 ms.



<u>**Figure 1**</u>: Spatiotemporal organization of (A) eating and (B) drinking in the pigeon, based on an analysis of individual motion picture frames taken at a speed of 100 frames/s. (From Zeigler et al., 1980).

3) **Mandibulation** begins after reclosure and involves a series of catch and throw movements during which the seed is moved from the beak tip to the back of the mouth.

4) **Swallowing** is initiated by contact of the seed with a specific region within the oral cavity and resembles mammalian deglutition. The spatio-temporal organization of eating is illustrated in Figure 1(A). For contrast, Figure 1(B) presents a similar analysis for drinking. Note that drinking involves a rhythmic alternation of beak opening and closing with a relatively small gape (Klein, LaMon and Zeigler, 1983).

Previous behavioral studies

Zeigler et al. (1980) used high speed cinematography to demonstrate that jaw-opening (gape) during pecking/grasping is directly proportional to seed size and that the adjustment is completed prior to contact of the beak with the target. In a subsequent study (LaMon and Zeigler, 1984) these observations were replicated and it was shown that the adjustment of gape size to seed size seen during feeding is also characteristic of conditioned keypecks with seed reinforcers. Pigeons pecking at a plain, transilluminated key emitted gapes which approximated the size of the preceding reinforcer. These data suggest that conditioning paradigms may eventually be useful in bringing pecking/grasping responses under experimental control.

A third study (Klein, Deich and Zeigler, 1985), was designed to clarify the behavioral mechanisms mediating the adjustment of gape size to target size. This adjustment could be mediated either by variations in the velocity of jaw opening, the duration of jaw opening or both. Increases in either of both of these with seed size could produce the observed relation between seed size and gape size. Variations in mean jaw opening velocity would presumably reflect activity in the jaw opener muscles. Variations in opening duration could be produced either by opening the jaw earlier in the peck or by varying the height of the head at the start of the peck or its mean velocity during descent. Cinematographic analysis indicated that while jaw opening latency is constant, both jaw opening mean velocity and duration vary directly with seed size. Analysis of correlations among these variables indicated that the processes mediating these effects differ for the two variables. Variations in jaw opening velocity with seed size reflect a direct relation between seed size and jaw movements. In contrast, increases in jaw opening duration are not produced directly but indirectly by increasing head height with seed size. Head height, in turn, controls the mean velocity of head descent. These observations suggested that the control of gape size during the opening phase of grasping involves two different effector systems: variations in jaw opening mean velocity are mediated by the jaw muscles; variations in jaw opening duration may also involve the neck muscles, which control head position.

The effector system

In contrast to mammals, the articulation of the avian jaw permits the independent movement of both the mandible and the maxilla. Jaw opening in birds is controlled by two muscle groups which operate upon the beak via a mechanical system of interacting bones and ligaments, the "kinetic apparatus" (Bock, 1964). In most birds, including the pigeon, elevation of the upper beak may be produced either directly or indirectly. Direct opening involves contraction of its opener muscle (M. Protractor Quadrati). Indirect opening is mediated by a "coupled kinesis" in which the contraction of the lower jaw opener (M. Depressor Mandibulae) acts upon the upper jaw via its relation with a postorbital ligament which functions to link the two jaws (Beecher, 1951; Bock, 1964). Thus jaw opening during grasping could be mediated by either a one-muscle or a two-muscle system. Behavioral data (Klein et al., 1985) showed that the elevation of the maxilla during grasping precedes depression of the mandible. This suggests that the opener of the maxilla may be active prior to loading of the postorbital ligament, so that the opener of the mandible does not contribute to maxillary elevation. This inference is supported by the observation that maxillary elevation continues to occur after section of the nerve to the M. Depressor Mandibulae so that the operation of this muscle is not necessary for upper jaw elevation. Taken together the behavioral and the denervation data suggest that the control of gape during grasping involves both opener muscles.

Similarities with reaching/grasping in humans

Comparison of pecking/grasping in pigeons (Deich et al., 1985; Klein et al., 1985) and reaching/grasping in humans (Jeannerod, 1981; Jeannerod and Biguer, 1982; Biguer, Jeannerod and Prablanc, 1982; Levine, 1982; Jeannerod and Prablanc, 1983) reveals some interesting similarities in topography and spatiotemporal organization:

1) Position-time and velocity-time profiles for transport components (reaching:pecking) are similar in shape in the two species, as are peak velocities (reaching 800 mm/s; pecking 520-970 mm/s). For both reaching and pecking the velocity of the transport component increases with distance from the target.

2) In both species, the topography of the prehensile organ (hand:jaw) during grasping is rather precisely adjusted to the stimulus characteristics of the target and this adjustment takes place prior to contact.

3) Movements parameters for the hand and jaw during grasping are similar. Both grip size (inter-finger aperture) and gape size (inter-beak aperture), increase with target size as do peak velocities, which are comparable in the two species (hand 300-400 mm/s; beak 237-290 mm/s).

4) In both species, separate sensorimotor channels may control the velocity of the transport and grasp components. Target distance controls the velocity of reaching and pecking; target size determines the velocity of the opening phase and grasping.

In addition to these functional and operational similarities, reaching/grasping in primates and pecking/grasping in the pigeon appear to be mediated by analogous neural systems. Both behaviors involve the processing of visual and somatosensory inputs by brain structures with access to efferent systems controlling axial and distal muscles. In mammals, control of these muscles groups is probably accomplished by largely separate (medial, lateral) descending pathways with limited overlap (Humphrey, 1979; Kuypers, 1981). There appears to be a comparable separation of descending pathways controlling axial and distal musculature in the pigeon. Neck motor neurons are located medially (Eden and Correia, 1982); jaw motor neurons, laterally (Wild and Zeigler, 1980). Jaw premotor neurons in the pigeon are located in the lateral (parvocellular) reticular formation (Berkhoudt et al., 1982) and linked to the forebrain via a descending pathway, the occipito-mesencephalic tract (OMT). OMT originates from the "somatosensorimotor" portion of the archistriatum (Zeier and Karten, 1971) and resembles in its course and distribution Bagley's bundle, a variant of the pyramidal tract arising in the pericentral cortex of ungulates (Haartsen, 1967). In view of the well documented contribution of the mammalian pyramidal tract to visuomotor behavior (Lawrence and Kuypers, 1968; Wiesendanger, 1981) it is of interest that lesions in OMT produce deficits in visuomotor behaviors involving the control of peck location and grasping (Levine and Zeigler, 1981).

These observations suggest that grasping in the pigeon approximates the functional complexity of primate grasping, involves similar sensorimotor control mechanisms and is mediated by analogous neural structures. These similarities in the organization of behavioral and neural processes mediating grasping in the two classes may reflect the fact that the pigeon's neck/jaw system faces many of the same problems of motor control as the arm/hand system of primates.

Why a kinematic analysis of grasping?

One of the main problems with which the central nervous system must deal is the enormous variety of movements the organism can emit. One way to solve the problem would be by means of a storage capacity sufficient to contain the activation and muscle sequences of every possible movement. But the storage capacity of the CNS is limited while the diversity of movements is unlimited. The CNS must have some mechanism to reduce the infinite movement capacity by constraining the modes of responding to wide situational variations (Bernstein, 1967). The neuromuscular activity must show some degree of constancy across situational variables, and such invariance should be expressed as constant relationships between kinematic and situational variables controlling movement. Thus an analysis of the kinematics of specific movements is a first step in clarifying the neural mechanisms mediating their control.

Current views on motor control mechanisms, have rephrased Woodworth's (1899) distinction between "initial adjustment" and "current control", distinguishing respectively, between "central motor programs" and the peripheral feedback responsible for the final adjustments. As Brooks (1979) has pointed out, targeted limb movements represent the combined action of two mechanisms. First, a preplanned initial impulse moves the limb towards the target, and second, in cases where there is time for an evaluation of the movement, corrections are implemented to rectify the trajectory. This leads to a distinction between "ballistic" (fast) and "ramp" (slow) movements (Richer, 1985; Hallett, Shahani, and Young, 1975; Desmedt and Godaux, 1978). A ballistic movement would be completely programmed and executed to its completion without peripheral feedback (open-loop) control, while slow movements could be influenced by peripheral feedback (closed-loop control).

A motor program is defined as the central representation of a sequence of motor actions which directs the movement as it is executed (Keele, 1981). The abstract representation that shares all the applications of the program specifies the objective and some constraints on the trajectory (Soechting and Lacquaniti, 1981). Within the framework of motor program theory, the role played by the kinematic invariants is viewed as the direct consequence of activation patterns of high level brain structures which are independent of the peripheral neuromuscular system (Schmidt, Zelaznik, Hawkins, Frank, and Quinn, 1979; Arbib, 1981).

Motor program theory and control of amplitude scaling.

The scaling of movement amplitude to stimulus characteristics is a general function of movement in both humans and lower animals. Theoretical accounts of response scaling generally assume that the initial (dynamic) phase of any movement involves the generation by motoneurons of an output (control) pulse whose properties determine the amplitude of contractions in relevant muscles. For rapid, targeted ("ballistic") movements the movement trajectory is assumed to be independent of peripheral feedback and to reflect some parameter of the control pulse which is determined (programmed) prior to the initiation of the movement. Such "pulse-step" models have been used to account for the relation between inputs and outputs in the operation of both skeletomotor and oculomotor systems (e.g., Robinson, 1964; Ghez, 1979). The use of the term "pulse" derives from the fact that when the slope of a change in a variable is constant, its first time derivative has the shape of a square pulse. When the slope of the movement is not constant, then the peak of the rate of change in amplitude (dA/dt) is a measure of the slope of the trajectory and thus is comparable to the height of the pulse.

Within a pulse control framework, we may distinguish two different control strategies:

1) Pulse height, when different amplitudes of a particular movement are produced by changes in the slope of the trajectory.

2) Pulse width, when different amplitudes are achieved by modulating the duration of the trajectory, leaving the slope constant. Some combination of these two strategies, i. e., control of both the slope and duration of the trajectory provides a third possibility.

A schematic representation of these two strategies is shown in Figure 2, in which trajectory vectors are represented for different movement amplitudes. Each vector connects the starting point of the trajectory with its end point. As the left hand portion of the figure indicates, different amplitudes can be achieved within the same rise time by changing the slope of the trajectory (pulse height control). Pulse width control is represented in the right hand portion of the figure in which increased amplitudes are achieved by increasing rise times, with the slope of the trajectory vector remaining relatively constant at different amplitudes.

Saccadic eye movements are generally characterized as being governed by a pulse-width strategy, in so far as saccade amplitude is controlled by the duration of an output pulse of oculomotor neurons which are firing at close to their maximum frequency (e.g., Robinson, 1970; Fuchs, Kaneko and Scudder, 1985). Targeted movements involving the skeletomotor system have been characterized as being controlled by a "pulse-height" strategy. For both isometric and isotonic contractions, various force levels are achieved by varying the velocity of the force trajectory (i.e., its rate of rise) while rise time remains essentially constant across a range of target forces (Freund and Budingen, 1978; Ghez , 1979; Ghez and Vicario, 1978; Gordon and Ghez, 1984).

Previous research on this problem has employed experimental procedures reflecting several types of methodological constraints.

1) Rapid movements: Tasks involving such movements are used because of the assumption that they do not involve peripheral feedback and are therefore more likely to reflect the operation of internal motor programs.

2) Isometric tasks: These are used to avoid interference from the inertial and elastic properties of the limb and muscles as well as from reflex responses to muscle activation

3) Scaling tasks: These are designed to elicit movements scaled to some property of the stimulus variable; e.g. scaling of movement trajectory to stimulus amplitude.

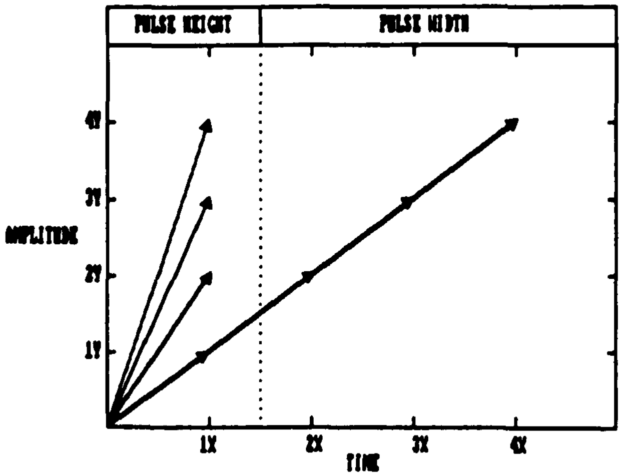


Figure 2: Schematic diagram illustrating the pulse height and pulse width strategies to describe the trajectory of a movement.

In the present study this approach to motor control mechanisms is extended to a very different type of behavior mediated by a different skeletomotor system: jaw movements during eating in the pigeon. As noted earlier, eating in this species involves several different motor patterns. One or more of these movements may require the scaling of jaw-opening amplitude to pellet (target) size. In this respect it is analogous to the scaling tasks used in motor control studies. While it is not an isometric task, this disadvantage is perhaps outweighted by the advantages of using an unconstrained, species-typical movement pattern. Providing an account of the kinematics of these movements would lay the foundation for subsequent studies of their neuromotor control.

The study was carried out in two stages. In the first part a descriptive analysis of the different jaw movements associated with the eating was carried out to determine which of the movements showed scaling of jaw opening amplitude to pellet (target) size. For those movements which did exhibit such scaling, a kinematic analysis of opening movement trajectories was carried out. Within the conceptual framework provided by the "pulse-control" model, the results of this analysis were used to clarify motor control mechanisms for each of the movement patterns.

GENERAL METHODS

Subjects

Six White Carneaux pigeons (**Columba livia**) obtained from a commercial supplier, were housed individually in a colony room with a 14:10 hours light dark cycle (on, 7:00 a.m.; off, 9:00 p.m.) and adapted to the laboratory for at least three weeks, during which food and water were continuously available. In the third week their free-feeding weight was computed by averaging their daily weight measured at the same time of the day. Birds were then food deprived until their weights dropped to about 80% of free-feeding value, at which point training was begun.

Apparatus

Training and testing were carried out in an operant conditioning chamber with walls and ceiling of 31x33x35 cm. in clear Plexiglass and a wire mesh floor. The front wall was painted black and contained the aperture of a specially designed food magazine. Pigeon pellets (ca. 3.2, 3.9, 4.9, 6.4, 8.7, and 11.1 mm.: Bioserv, Summit, New Jersey) were delivered by a universal dispenser into a feeder made from a standard watch glass. Activation of a solenoid raised the feeder into position for pellet delivery. At the end of each pellet presentation (trial), the cup was lowered into a receptacle to dispose of any remaining pellets and insure an empty cup at the start of the next presentation. The chamber ceiling was modified for the insertion of a mercury swivel (Scientific Prototype). The test chamber was located within an acoustically shielded outer chamber and a 25 w houselight provided general illumination.

Behavioral testing procedures

Prior to testing a series of training sessions was given to insure prompt response to the target stimuli (food pellets). The birds were then mounted (under light Equithesin anesthesia) with the Hall-effect device and magnet (Figure 3) and testing was begun within 48 hrs.

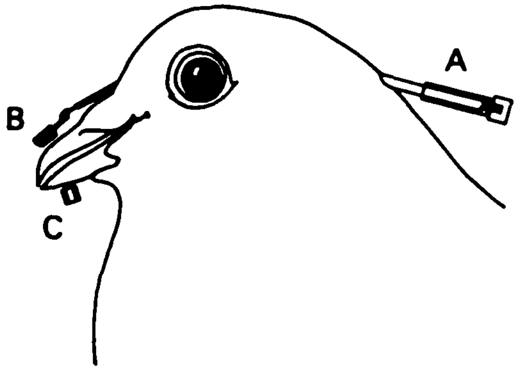


Figure 3: Schematic diagram showing the position of the Hall-effect IC (B) and magnet (C) on the upper and lower beaks, as well as the electrode assembly (A) used to connect the IC chip to the mercury swivel.

Each daily test session consisted of the non-contingent presentation of 30 pellets, one at a time, grouped by blocks of 5 pellets of the same size and generally presented in the order 4.9, 3.2, 3.9, 6.4, 8.7 and 11.1. On each trial a pellet remained available for six s. after delivery. Trials were separated by an intertrial interval of 10 s. Each subject was tested for a minimum of four sessions. The behavior of individual subjects was carefully observed during testing using a closed-circuit video system.

"On-line" monitoring of jaw movements

Jaw opening and closing movements were transduced using a Hall-effect integrated circuit (Panasonic IC # DN6835) which generates a voltage monotonically related to the strength of an applied magnetic field. By mounting the Hall-effect device on the upper beak and a samarium-cobalt magnet on the lower beak,a continuous voltage output which is proportional to the pigeon's gape (i.e., the distance between the two beaks) can be obtained. The Hall-effect device is linked to the monitoring system via a connector through the mercury swivel. Proximity of the pigeon's head to the feeder was monitored by a second Hall-effect device located beneath the watch glass. Analogue voltages from both devices were amplified and transformed into digital signals by an A/D interface (National Semiconductor). The reliability of the Hall-effect measuring system was tested by comparing records obtained under this system with others obtained by an oscilloscope. Both records showed the same voltage fluctuations within the same temporal frame work.

At the start of each test session the system was calibrated using a series of digital readouts obtained, first, with the jaws fully closed and then with the jaws opened to varying degrees by the insertion of of a graded series of spherical stimuli including the six Bioserv pellet sizes and a 20 mm pith sphere. During each session pellet delivery initiated reading of the A/D values (sampling rate: 4 ms) for a period of 6 s. When gape exceeded a 2 mm threshold (i.e. approximately double of the resting level) the previous 400 ms and the subsequent 1600 ms of data were stored to disk. If no response was produced the trial was terminated and a "no response" stored for that trial.

Data acquisition and conversion as well as control of pellet delivery were carried out by an Apple IIE microprocessor programmed in the First language (Scandrett and Gormezano, 1980). The monitoring system has been described in detail elsewhere (Deich, Houben, Allan, and Zeigler, 1985a). The First data were converted to IBM Basic via a specially written communications program (Allan, Bermejo and Houben, 1986). Classification of jaw movement types and data analyses were conducted using an IBM PC microcomputer programmed in Compiled IBM Basic.

PART I: DESCRIPTION AND CLASSIFICATION OF GAPE TYPES

INTRODUCTION

Qualitative description

Figure 4 presents a typical record of jaw movements monitored by the Hall-effect system during an eating response sequence in the pigeon. Several distinct types of jaw movements may be identified and associated, on the basis of previous cinematographic analysis, with specific components of the eating response (see General Introduction).

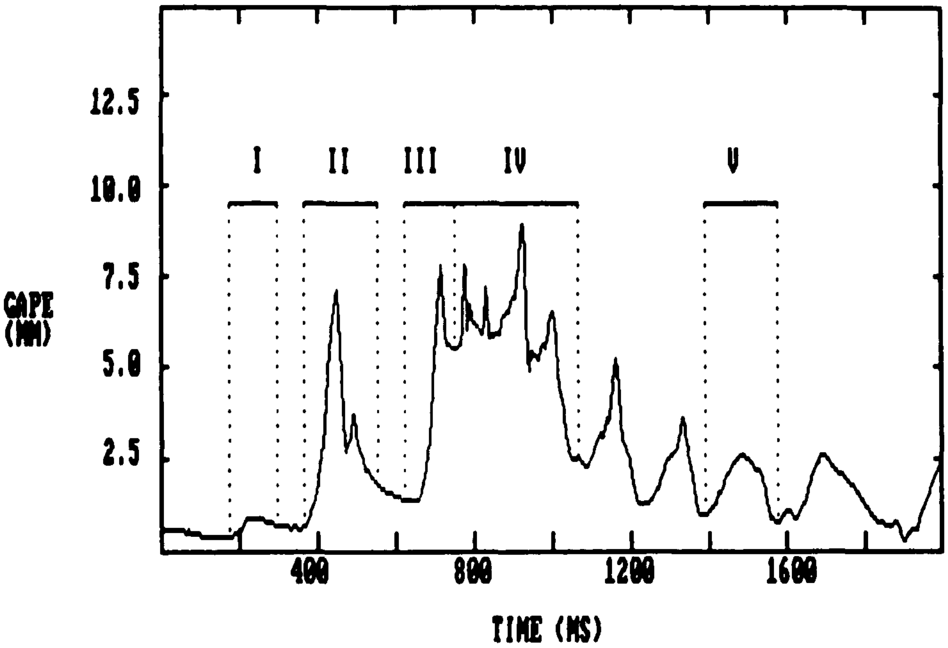


Figure 4: Computer record of jaw movement during standard two seconds trial. The record is representative of a 6.4 mm target size. I: Prepeck; II: Unsuccessful grasp; III: Successful grasp; IV: Mandibulation; V: Swallowing.

The record begins with a period of maintained jaw opening of very low amplitude which reflects the distance between the beaks prior to the initiation of the eating sequence (resting gape). The first jaw movement seen is a small perturbation in the record (**prepeck**) followed by a **grasp**. The record illustrates two types of grasp. The first type (**unsuccessful**) terminates with a reclosure whose gape approximates the resting level of jaw opening. A second (**successful**) grasp terminates with a reclosure closely approximating the pellet size, ingestion of the pellet, and a period of repetitive opening and closing of the jaw (**mandibulation**) during which the pellet is transported from the beak tip to the back of the oral cavity. **Swallowing**, the last event in the jaw movement record, involves a series of opening/closing movements, considerably larger than prepecks but of lower amplitude than the movements associated with grasps or mandibulation.

Thus the pigeons' eating behavior comprises four identifiable classes of **jaw movement**. Each of these classes involves both an opening and a closing movement. The focus of the present study will be on **jaw-opening**. Figure 5 presents movements associated with each class for all six subject. They were selected from a group of 90-100 eating sequences from each subject, and ordered by size within each pellet type. For comparison, successful and unsuccessful grasps are plotted separately. As a starting point for subsequent analysis, we examined each of these movement classes in some detail.

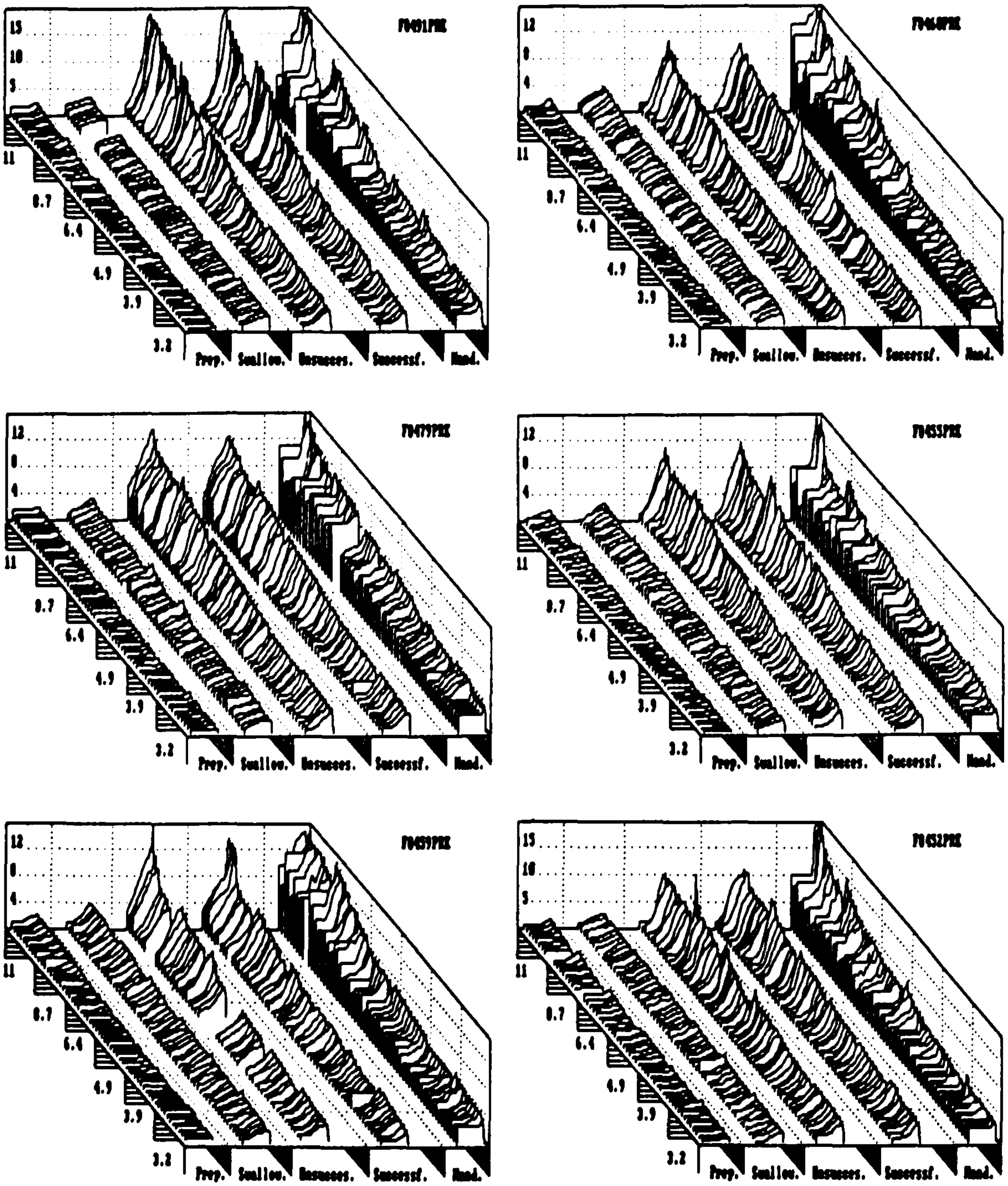


Figure 5: Tridimensional plots representing the raw data from all six subjects classified by gape type and size. The data represent the majority of movement trajectories used in the analysis. X-axis: peck type; Y-axis: amplitude (in mm); Z-axis: target (pellet) size (in mm)

Classification of gape types

Throughout this analysis a distinction was made between amplitude and gape measures. Gape is a measure of interbeak distance and is equal to the gape at the start of the movement (**initial gape**) plus the amplitude of the opening movement. Amplitude is a measure of interbeak displacement during the jaw-opening period. Thus for any stimulus value, gape will always be equal to or larger than amplitude. Since the focus of interest is on beak displacement (jaw opening movement) the appropriate measure is amplitude rather than gape.

METHODS

Preliminary analysis of a large number of trials revealed that gapes could be divided into 5 different classes, each associated with a different type of jaw movement. A computer-assisted scoring program was created to retrieve and display individual trials in order to select and classify these different types of gapes. The computer read each of the data points that constituted the trial, and stopped when it detected a beak movement, as defined by the presence of a set of three inflection points, querying the scorer to indicate under which category to include it. The algorithm for identifying the inflection points included three criteria. First, the beginning of an opening movement (initial gape), was defined by three consecutive changes of increasing value. Second, the next inflection point (peak gape) was identified either by a decreased value or by three consecutive equal values. Third, the end of the closing movement (reclosure), was detected either by the initiation of a new opening movement or the absence of beak movement (three consecutive equal values). The computer then stored the 33 points preceding (132 ms), and the 17 points (68 ms) following peak gape, under the appropriate movement class

A more restrictive criterion was applied to detect the inflection points during mandibulation, in order to minimize the obscure effects of small irregular fluctuations. To deal with this problem the scoring program looked solely for those inflection points in which the amplitude of the movement (peak gape minus starting gape) was greater than 0.5 mm. Only one of these mandibulations was chosen as representative of the whole mandibulation sequence, the highest once the first and the last mandibulations within the same peck were discharged.

Based on observations made during the trial, a small number of atypical pecks (about 5%) were left unscored. These included pecks at pellets outside the cup, pecks directed to the side, rather than from above, pecks obscured by interference from the head proximity signal, and pecks so close to each other that their boundaries were ambiguous.

In order to use for the analysis pecks produced under the best training conditions, sessions were scored in reverse order, starting with the last one, until a population of at least 10 successful eating sequences (and therefore including at least 10 successful grasps) for each pellet size were scored. If within this population of eating sequences 10 or more movements for each of the other 4 categories were acquired, the scoring process was terminated. If not, scoring was continued until sufficient movements (at least 10) were acquired within each type. Scored movements were saved for analysis on separate data files, one for each movement type and subject.

Scoring reliability was tested by computing the correlations among four different scorers for each of the gape types. Spearman correlations were in all instances higher than 0.9.

RESULTS

For each of the movement classes defined in Figure 4, the frequency distribution of movement amplitudes was examined to determine whether it varied with pellet size. Next, trajectories for each movement type were plotted to indicate the range of amplitudes involved and the extent to which the form of the trajectories was similar for different pellet sizes and for individual subjects. Finally, functions relating amplitude to stimulus size were plotted and a statistical analysis of these data carried out.

The statistical analysis was based upon a sample of at least 10 movements for each target size. Pearson's correlation coefficients and anovas were computed to explore both the presence of a proportional scaling of amplitude to target size, and the significance of the difference among the values for the six pellet sizes. Epsilon coefficients were obtained from the anovas, as a measure of comparing both tests under some similar parameter, given that the epsilon coefficient bears the same relationship to the "F" statistic that Pearson's "r" coefficient bears to the "t" statistic.

Grasps

Figure 6 presents frequency distributions of opening amplitudes for both successful and unsuccessful grasps summed across all six subjects. For both types a shift in pellet size is reflected in a shift in the peak of the amplitude distribution. Superimposing the two distributions produces, for any given pellet size, an almost perfect match, confirming their essential similarity. There is a strong suggestion of amplitude scaling for both grasp types and this is confirmed by an analysis of functions relating pellet size to grasp amplitude for the two types of grasp in three individual subjects (Figure 7).

For both grasp types the functions appear essentially linear, and approximate the perfect scaling of peak amplitude to target size. Table 1 presents correlation coefficients and F values for each of the birds and for both types of grasps. The range of correlations is similar for the two groups and all correlations are highly significant ($p < .0001$). A comparison of amplitude functions for the two grasp types (Figure 8) shows they almost completely overlap.

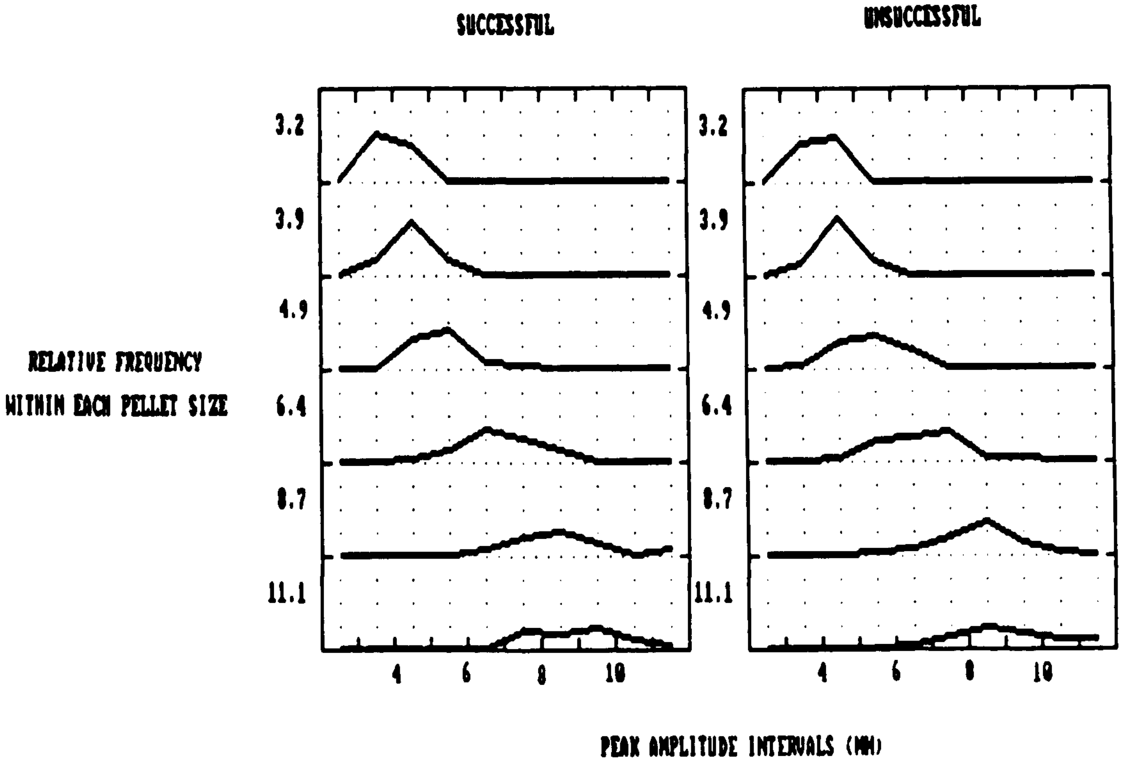


Figure 6: Relative frequency polygon of peak amplitude distribution for both successful and unsuccessful grasps. The Y-axis represents relative frequency in units from 0 to 100 (for each target size), and the X-axis intervals of amplitude of the jaw movement. Data are based upon more than 60 grasps for every pellet size summed across all birds.

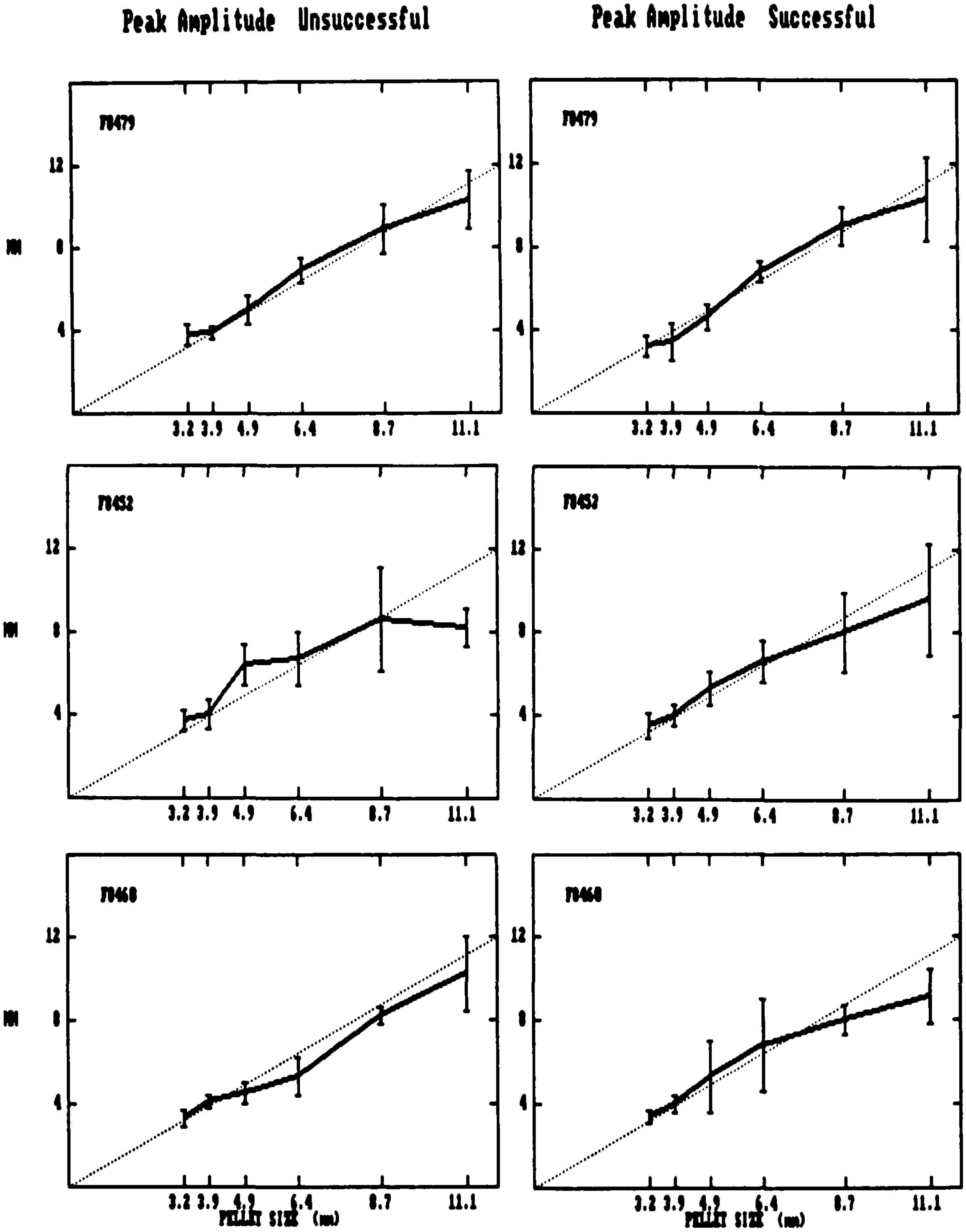


Figure 7: Peak amplitude as a function of pellet size, for three birds, comparing their successful versus unsuccessful grasps. Dotted line represents the 1:1 ratio between peak amplitude and pellet size. Vertical lines represent standard deviations.

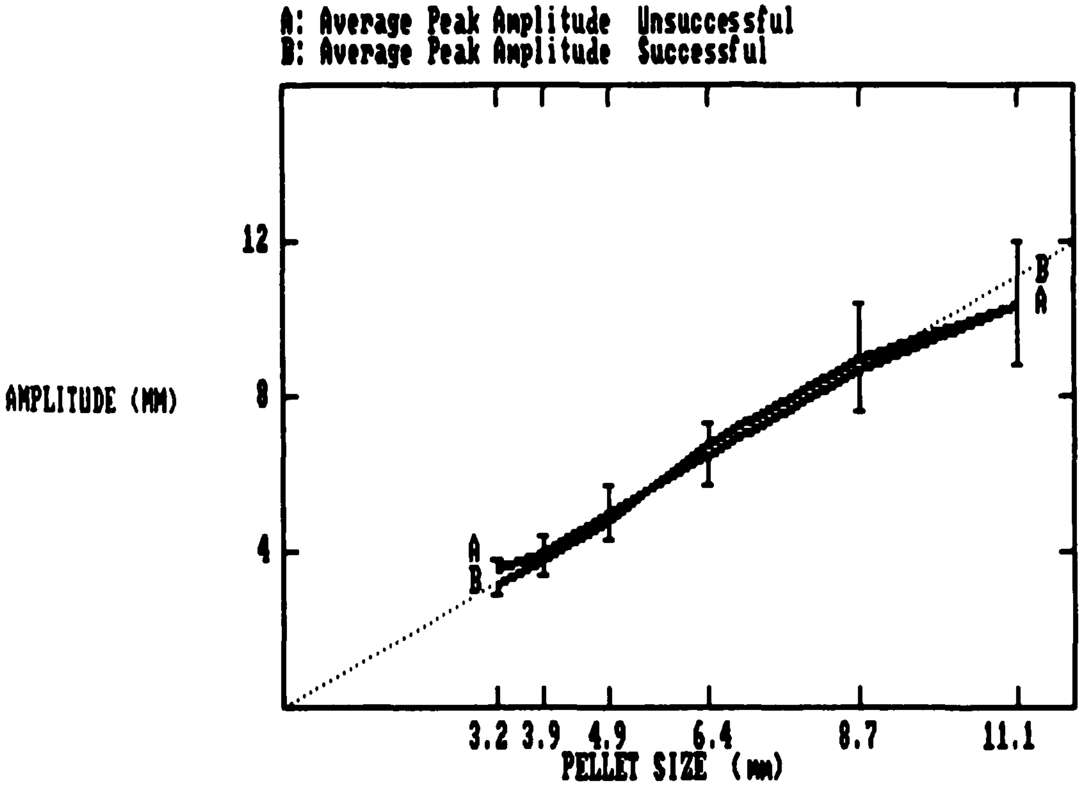


Figure 8: Average functions relating peak amplitude to target size for successful and unsuccessful gapes across all six birds. Vertical lines represent standard error of the means. A: Average peak amplitude for unsuccessful grasps; B: Average peak amplitude for successful grasps.

Table 1: Correlations and anovas between target size and peak amplitude for successful and unsuccessful grasps, for all six subjects. Mean values were computed using Fisher's Z transformation.

		Correlation		Anova		
Grasp Type	**Bird**	r	p	F	p	e
Unsuccessful	F8452	.72	<.001	28.53	<.001	.79
	F8455	.90	<.001	81.80	<.001	.91
	F8459	.84	<.001	21.72	<.001	.83
	F8460	.93	<.001	95.75	<.001	.93
	F8479	.93	<.001	150.27	<.001	.93
	F8491	.89	<.001	75.29	<.001	.89
	Mean	.90				
Successful	F8452	.82	<.001	33.41	<.001	.81
	F8455	.82	<.001	46.11	<.001	.86
	F8459	.84	<.001	29.97	<.001	.83
	F8460	.84	<.001	33.66	<.001	.84
	F8479	.92	<.001	100.39	<.001	.93
	F8491	.87	<.001	47.04	<.001	.87
	Mean	.88				

Figure 9 presents movement trajectories for the grasps of three of the subjects. Each trajectory was obtained by averaging 10-20 unsmoothed single trajectories after aligning them by the peak amplitude point. For both grasp types, the curves seem quite similar.

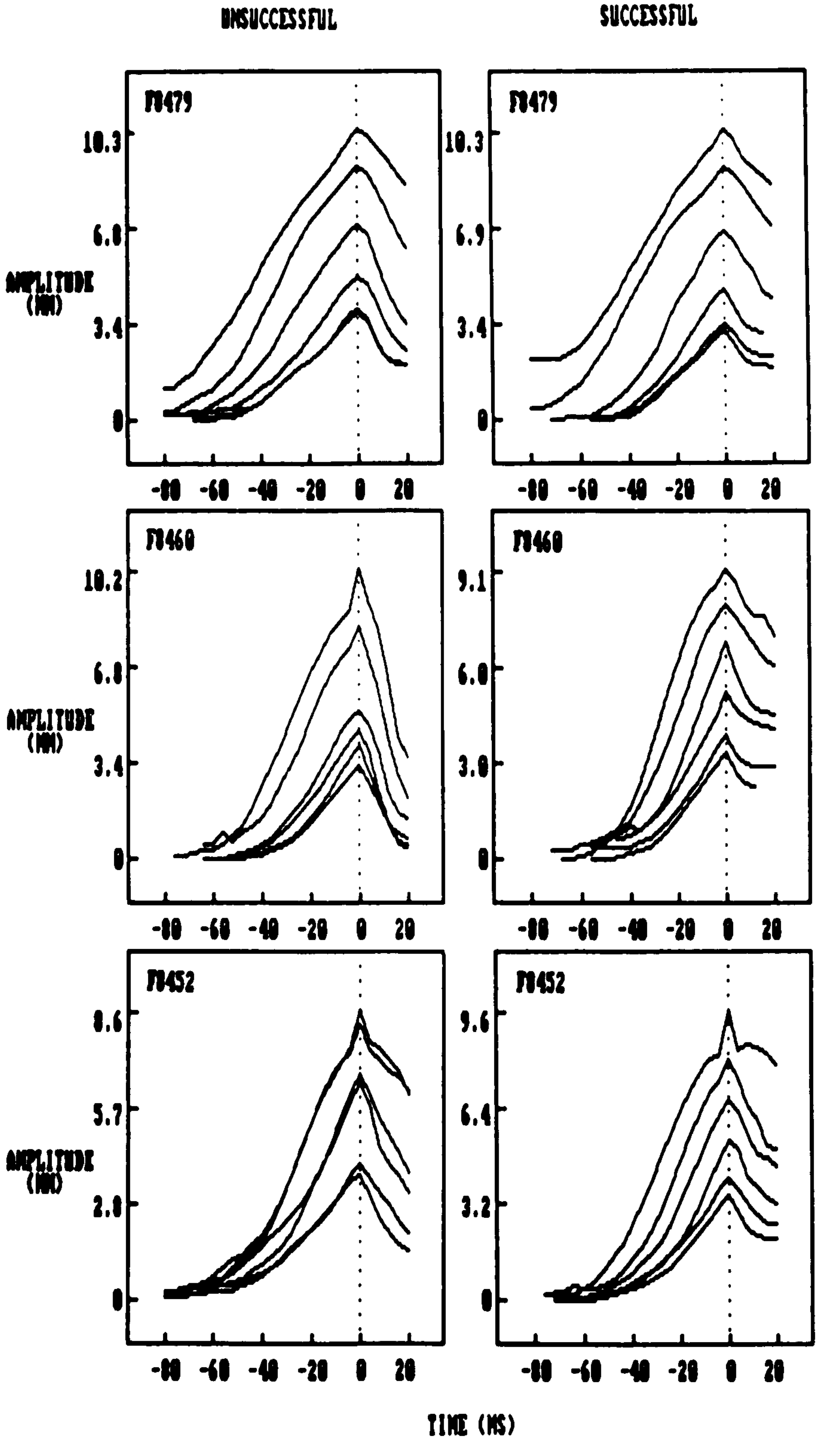


Figure 9: Successful and unsuccessful opening trajectories during grasping for independent pellet sizes in three birds. Trajectories are aligned with respect to their peak amplitudes, and were obtained from the raw data. Each trajectory represents the mean of at least 10 individual opening trajectories.

Mandibulation

Figure 10 presents frequency distribution of opening amplitudes for jaw-opening movements associated with mandibulation, summed across subjects. The data suggest some degree of shift in the peak of the distribution with increasing pellet size. The existence of a relationship between pellet size and amplitude is confirmed by the functions plotted for individual birds in Figure 11 and by the accompanying statistical analysis (Table 2). Correlation coefficients, though smaller than those for grasps are all highly significant (p<.001). Figure 12 presents movement trajectories for each of the six subjects.

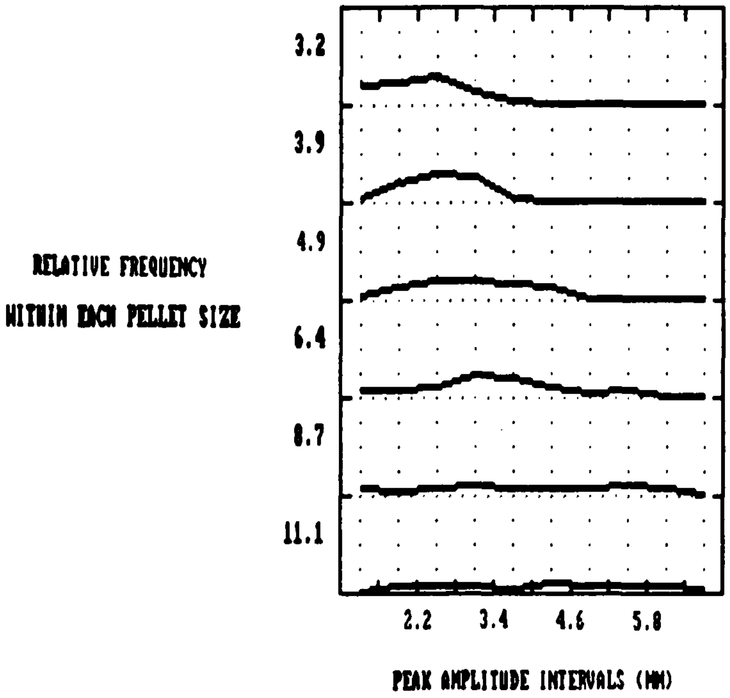


Figure 10: Relative frequency polygon of peak amplitude distribution during mandibulation. Data are based upon more than 60 responses for every pellet size.

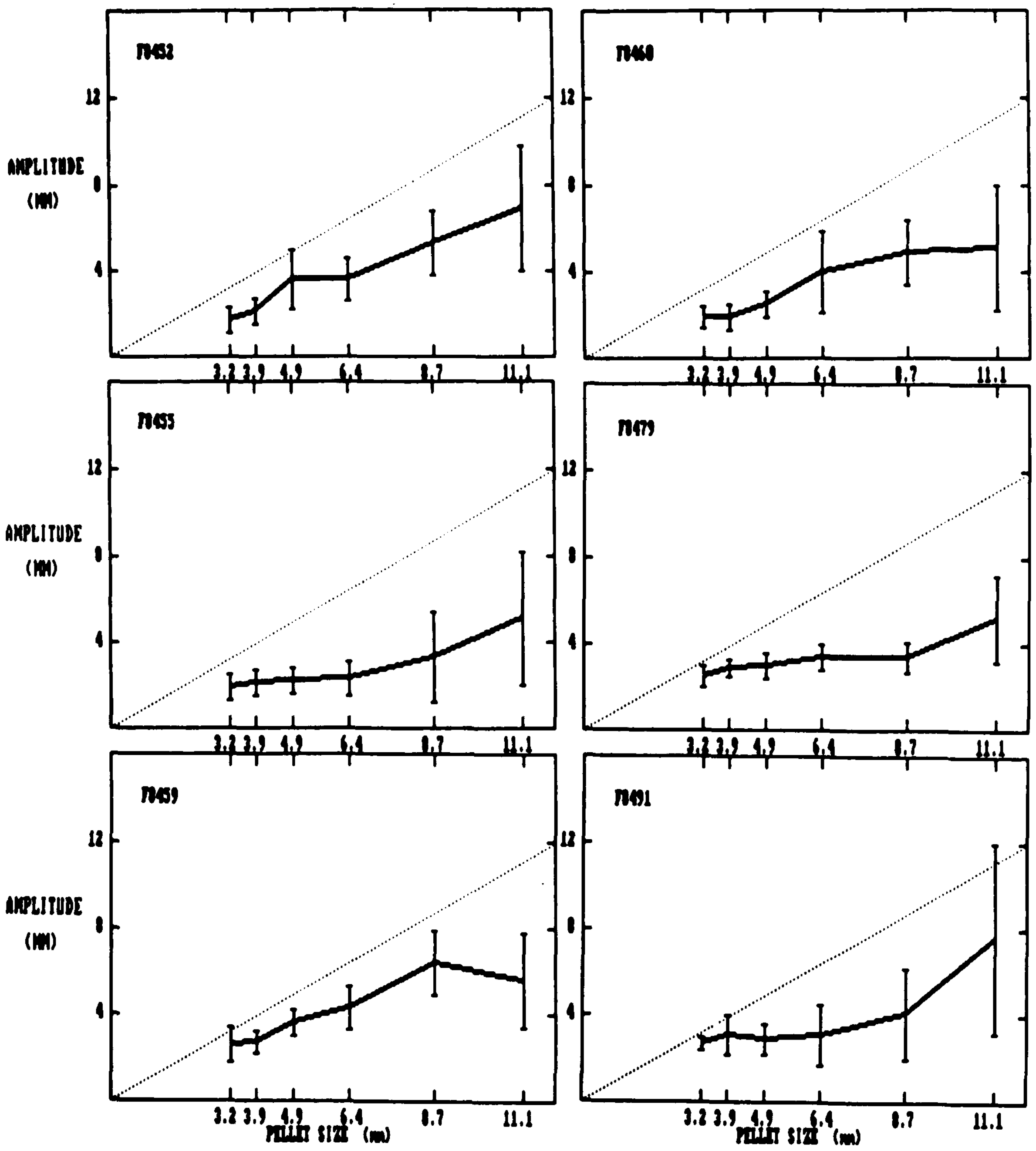


Figure 11: Peak amplitude as a function of pellet size, during mandibulation, for each of the six birds.

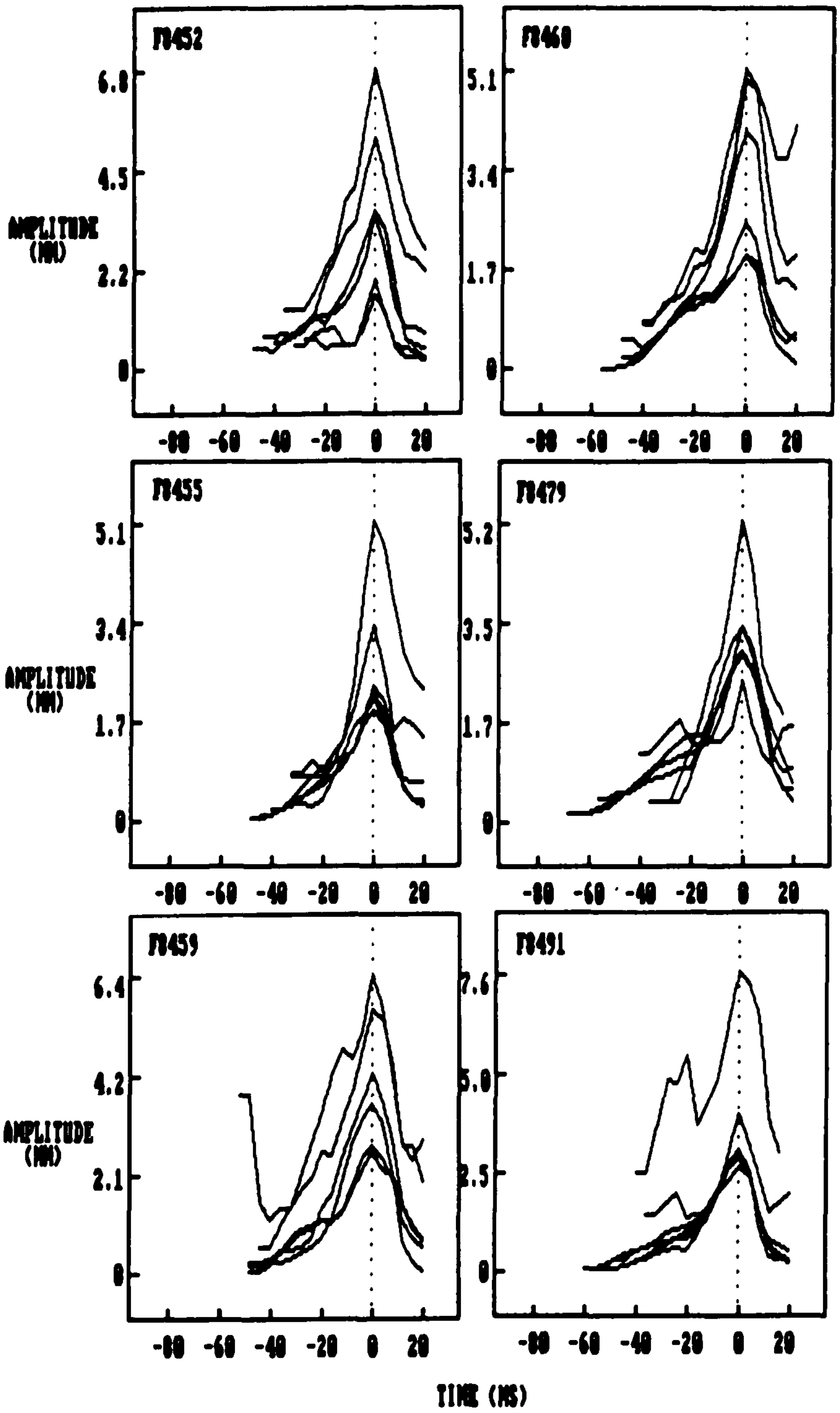


Figure 12: Mean amplitude trajectories during mandibulation for each one of the six birds. Trajectories are aligned according to their peak amplitudes and obtained from the raw data.

Table 2: Anovas and correlations for peak amplitude with target size, during mandibulation. Legend as in table 1.

		Correlation		Anova		
Mandibul.	Bird	r	p	F	p	e
	F8452	.75	<.001	20.44	<.001	.74
	F8455	.53	<.001	6.42	<.001	.52
P. Amplitude	F8459	.70	<.001	16.28	<.001	.74
	F8460	.64	<.001	9.71	<.001	.63
	F8479	.62	<.001	11.26	<.001	.64
	F8491	.53	<.001	7.63	<.001	.58
	Mean	.63				

Prepecks

Figure 13 and 14 present respectively frequency distributions and amplitudes of prepeck opening movements. For neither does there appear to be a systematical relationship with pellet size. Although the pellet size varies across a range of more than 8 mm, prepeck amplitudes vary across a range of less than 1 mm. The results of the statistical analysis are shown in Table 3. Figure 15 presents movement trajectories of the prepecks of individual subjects.

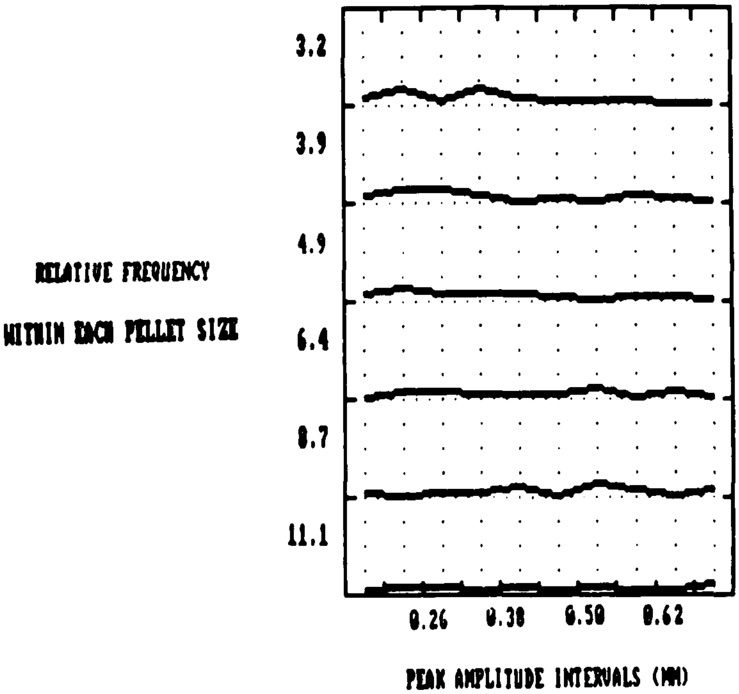


Figure 13: Relative frequency polygon of peak amplitude during prepecks for each target size. Plots are based upon a minimum of 60 gapes for each pellet size, taken all subjects.

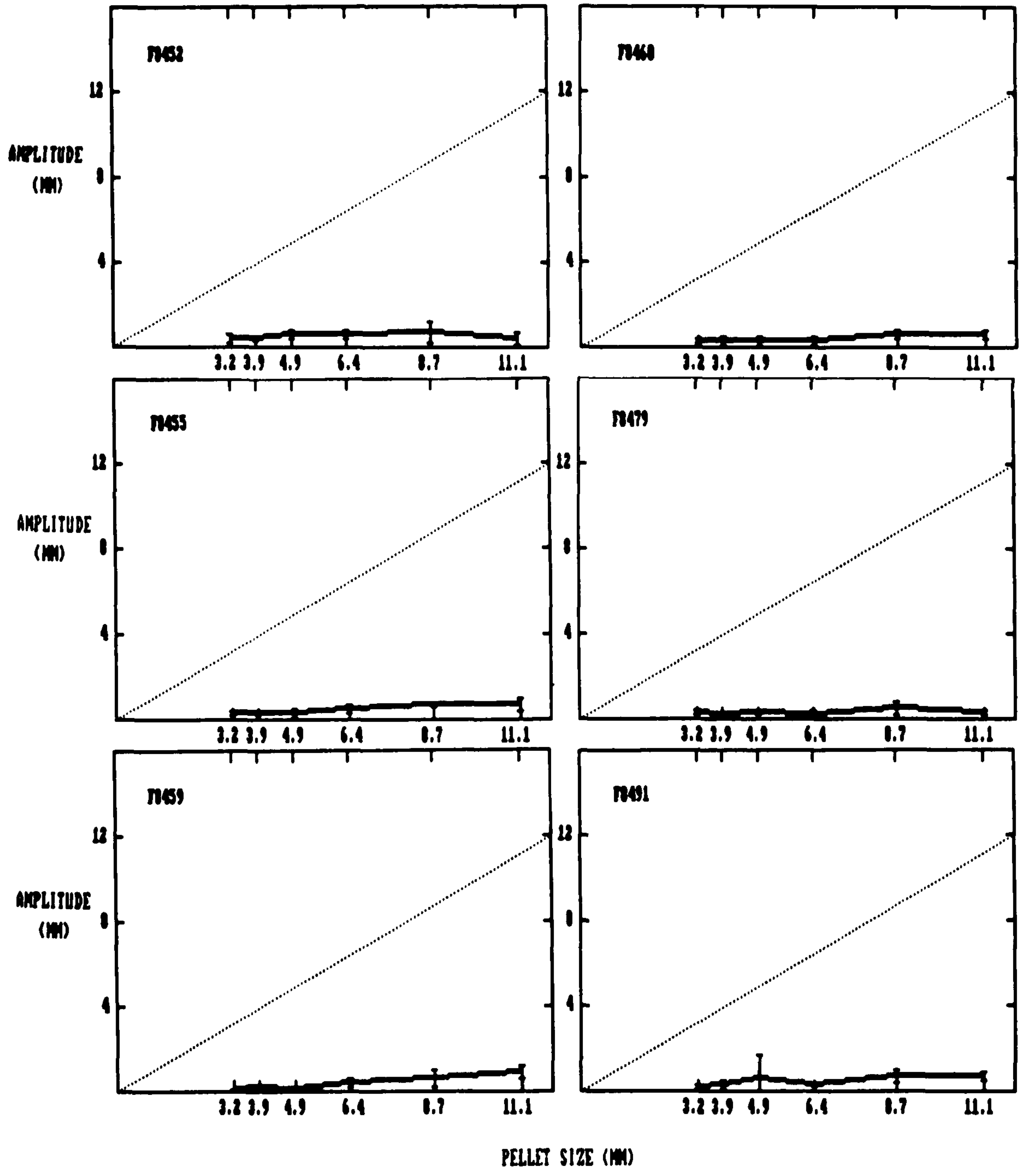


Figure 14: Individual peak amplitude function with target size for prepecks. Standard deviations are plotted over the means.

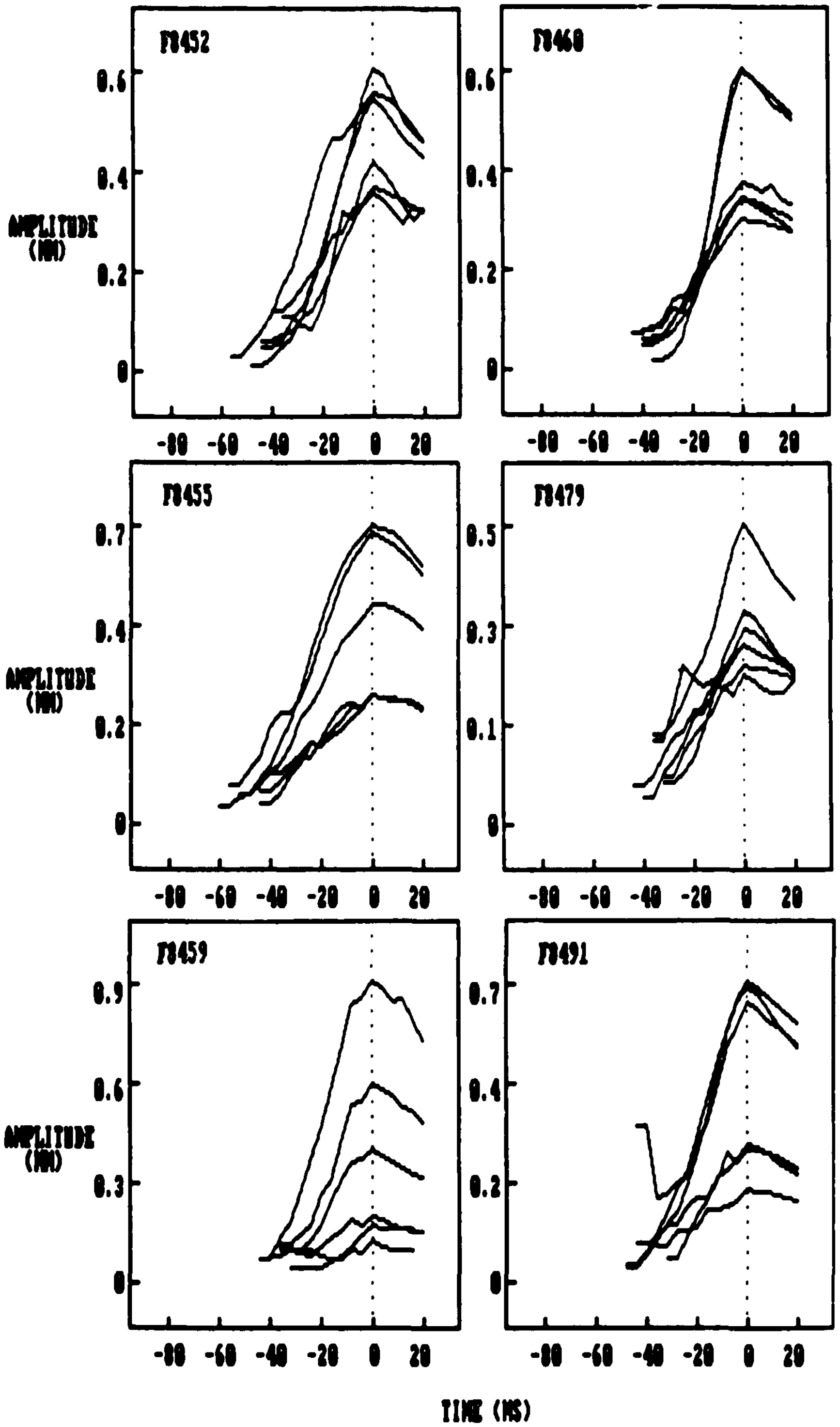
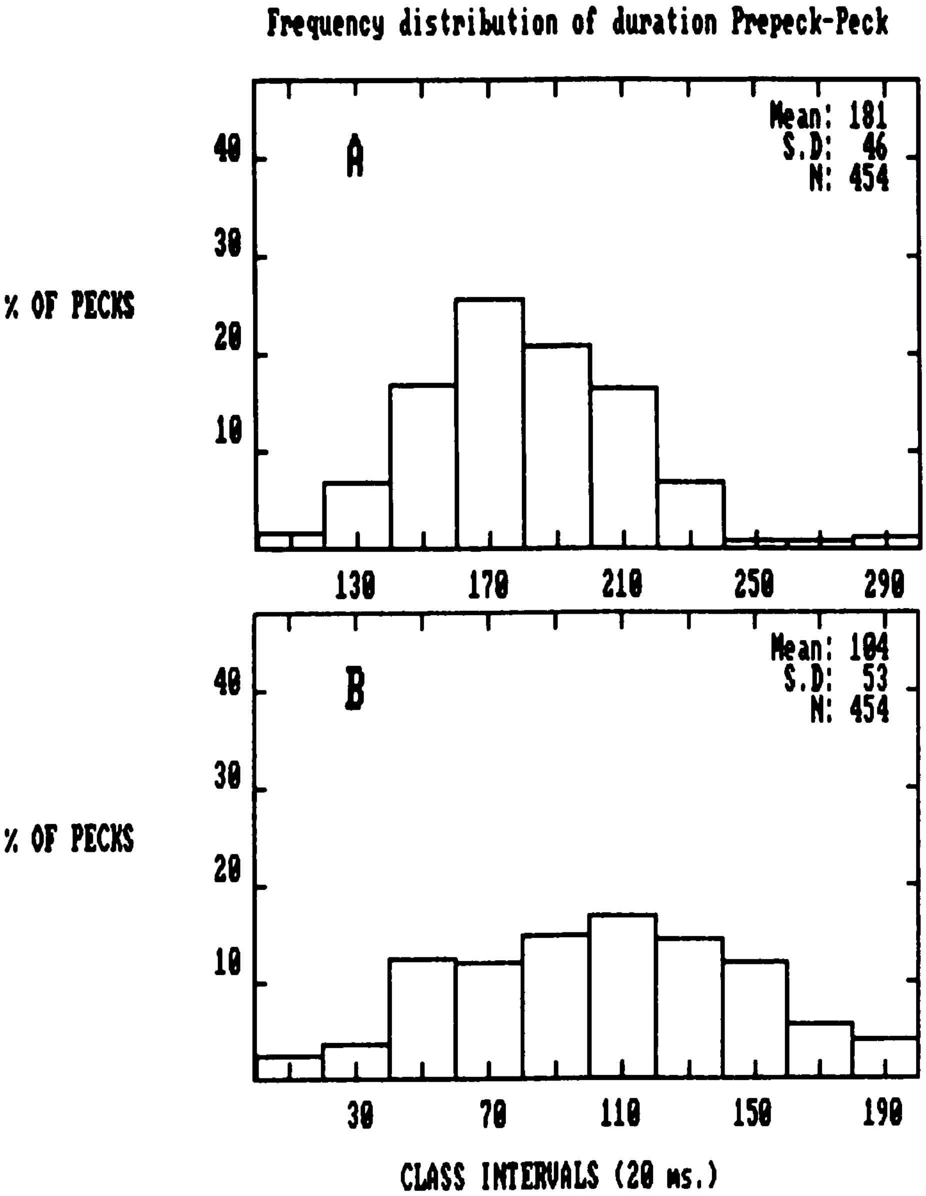


Figure 15: Mean amplitude trajectories for each of the six birds across target sizes. Trajectories are aligned with respect to their peak amplitudes.

Table 3: Correlations and anovas between peak amplitude and pellet size for prepecks. Legend as in table 1.

	Correlation		Anova		
Bird	r	p	F	p	e
F8452	.16	N.S	2.2	N.S	.28
F8455	.59	<.001	10.72	<.001	.60
F8459	.71	<.001	14.37	<.001	.70
F8460	.46	<.001	4.57	<.01	.43
F8479	.21	N.S	2.67	N.S	.30
F8491	.25	N.S	2.01	N.S	.26
Mean	.42				

Inspection of a large number of eating sequence records suggested that prepecks occurred in a fairly consistent temporal relation with respect to the subsequent grasp. To clarify the nature of this relation we examined frequency distributions of two sets of time intervals: (A) between the onset of prepecks and the onset of the following grasp, and (B) between prepeck offset and the onset of the subsequent grasp. The distributions are presented in Figure 16 and represent the data of all six birds. The results will be discussed later.



<u>**Figure 16**</u>: Frequency distribution histogram showing time relationships between prepecks and the subsequent grasp. (A) from onset to onset; (B) from end to onset.

Swallows

Figures 17, 18, and 19 present respectively, frequency distributions, functions relating amplitude with target size, and trajectories for jaw opening amplitudes associated with swallows. The distributions are uniform and do not appear to vary with target size. No systematic relation between amplitude and target size is evident in Figure 18 which presents functions for each of the birds. The movement trajectories shown in Figure 19 are very similar across both pellet sizes and individual birds. As for prepecks, half of the birds show significant correlation with pellet size, the other half do not (Table 4).

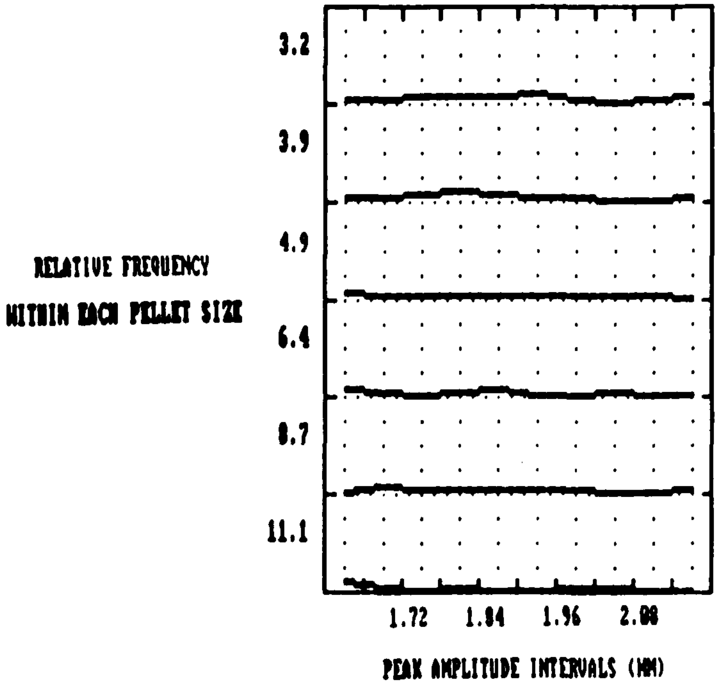


Figure 17: Relative frequency polygon for peak amplitude, during swallows, for each of the six target sizes. A minimum of 60 gapes were used in the computations for each pellet size.

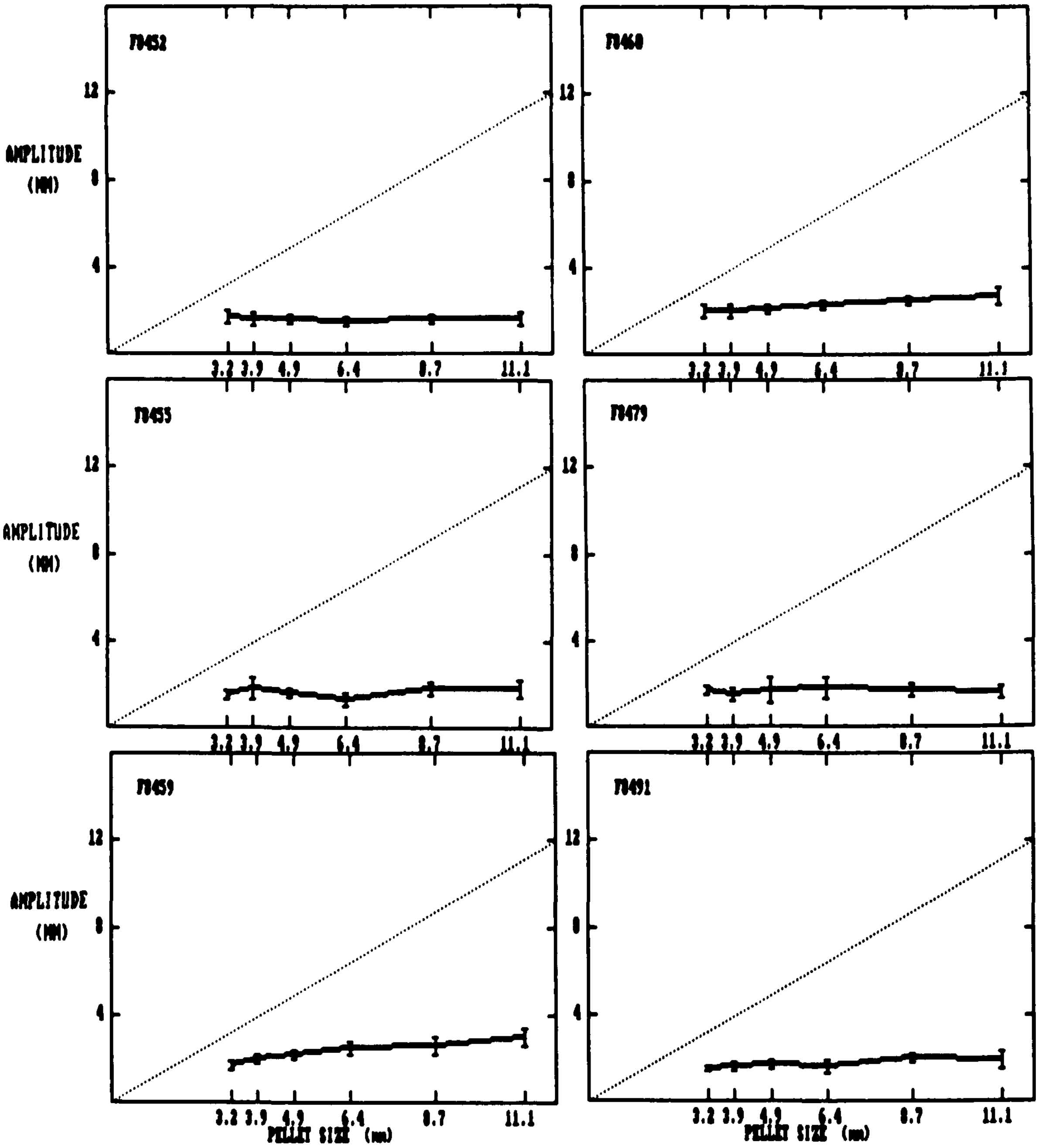


Figure 18: Individual peak amplitude functions related to target size for swallows. Standard deviations are plotted over each mean.

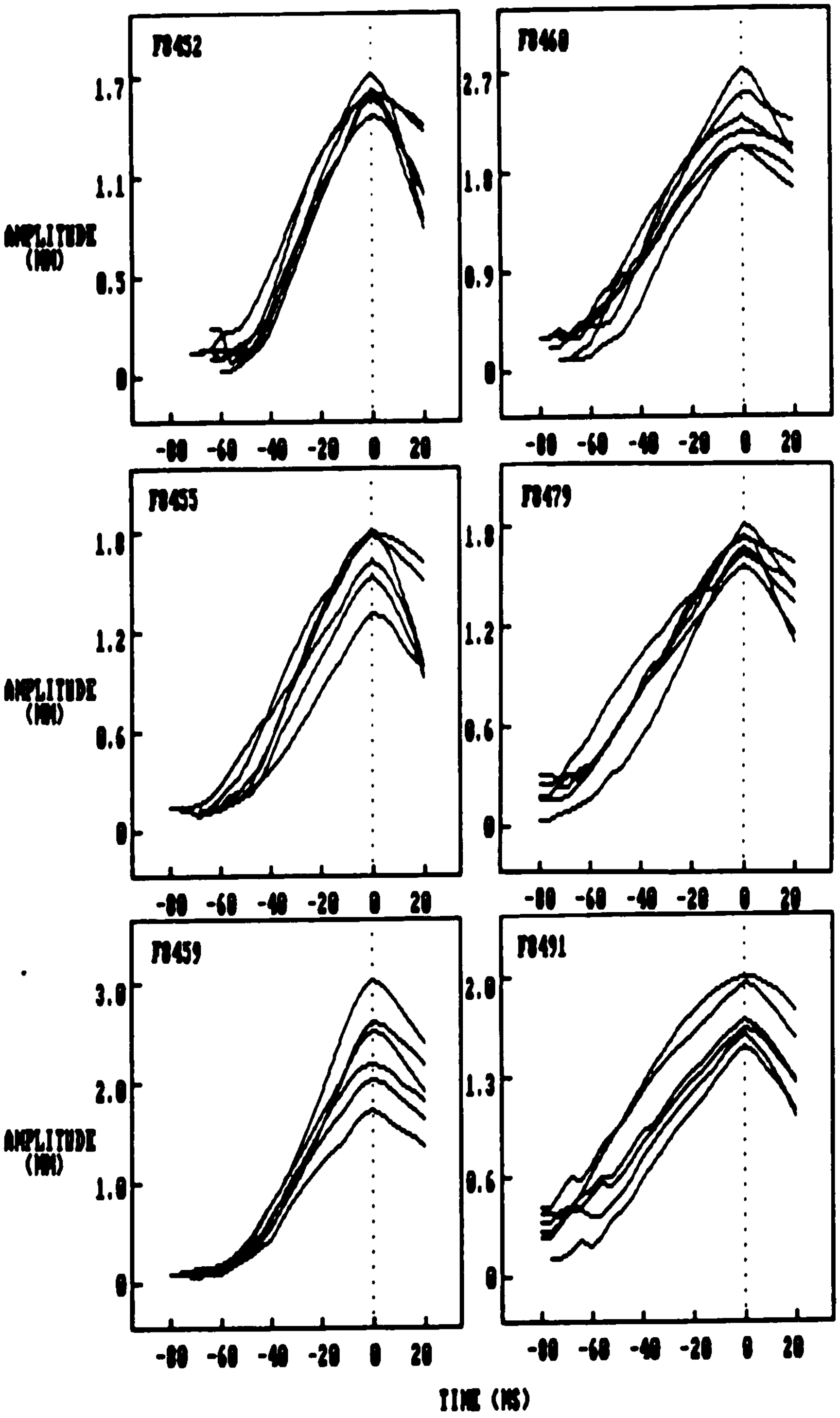


Figure 19: Mean amplitude trajectories for each of the six birds and, within them, for every target size. Trajectories are aligned with respect to their peak amplitudes.

Table 4: Correlations and anovas for peak amplitude of swallowing gapes. Legend as in Table 1.

	Correlation		Anova		
Bird	r	p	F	p	e
F8452	-.07	N.S	1.07	N.S	.06
F8455	.15	N.S	3.60	<.010	.38
F8459	.75	<.001	19.69	<.001	.76
F8460	.65	<.001	8.93	<.001	.61
F8479	.01	N.S	.54	N.S	.00
F8491	.48	<.001	5.12	<.001	.47
Mean	.35				

Inspection of the Hall-effect records suggested that, in addition to the amplitude scaling of jaw-opening, jaw movements during mandibulation may possess several additional characteristics of interest for the analysis of motor control mechanisms. These are illustrated in Figure 20, which superimposes a series of Hall-effect records obtained, for a single subject during the mandibulation of each of five different pellet sizes. The figure suggests that the number of mandibulations and the duration of the mandibulation component increase with pellet size. This hypothesis was tested by plotting the duration of mandibulation and the number of mandibulations as a function of target size for each of the birds. An analysis of variance indicates that for both measures this increase is significant at or beyond the .05 level. Because the individual functions were similar the data were combined and group means are plotted in Figure 21.

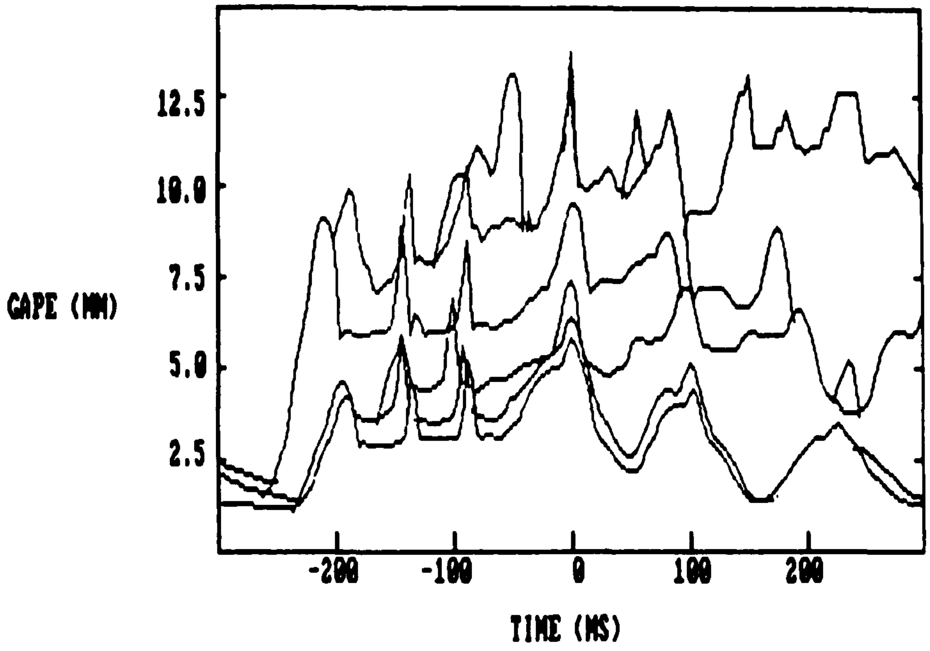


Figure 20: Jaw movements during mandibulation associated with different target sizes (for a single bird). Records are in progressive order from the bottom (smallest target size) to the top (biggest target size).

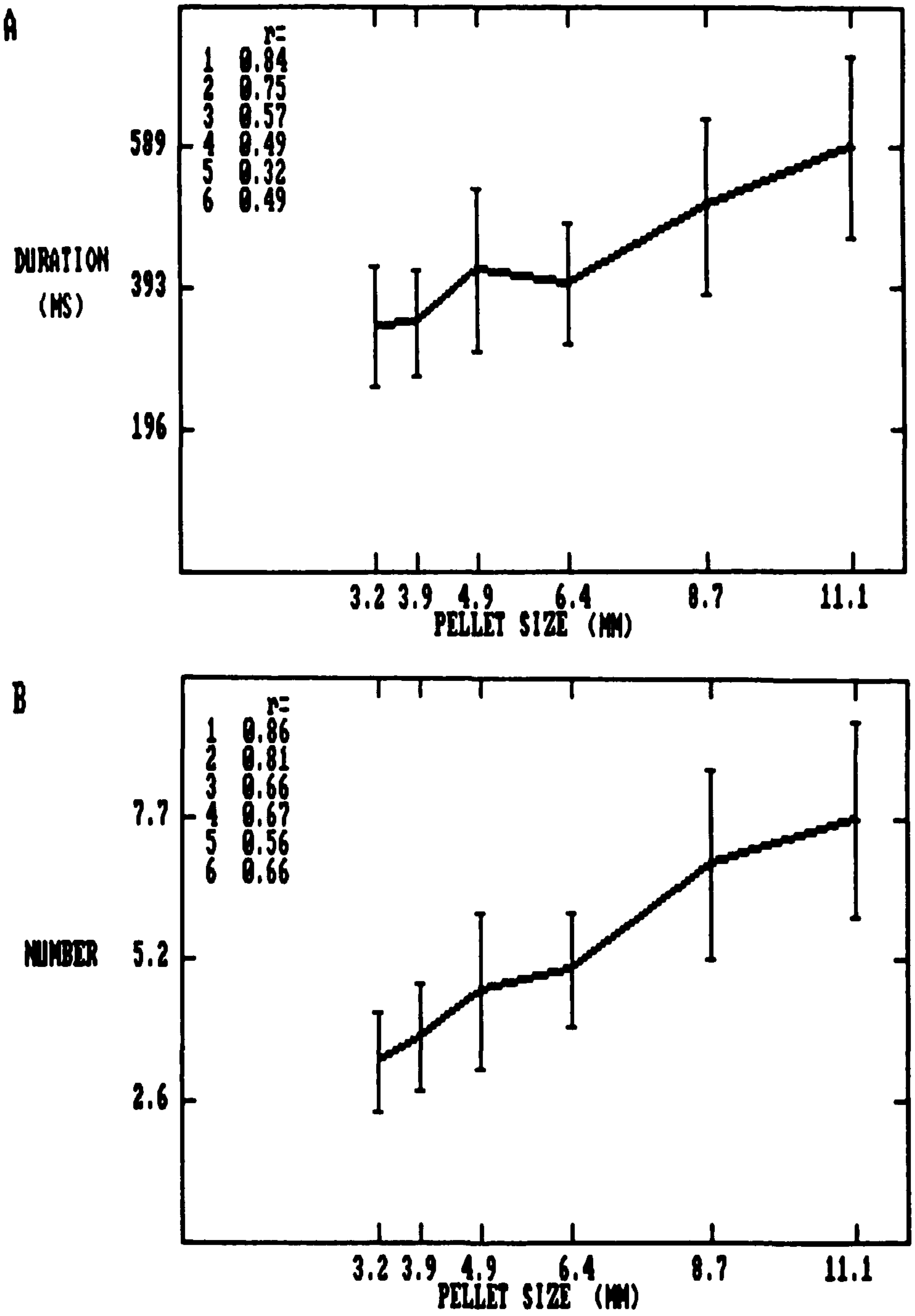


Figure 21: Duration of the mandibulation component (A), and number of mandibulations (B) as a function of target size. Functions were obtained as average of all subjects.

Examination of the individual records in Fig. 20 also suggests that gapes during mandibulation fall into two different populations with respect to amplitude. There is a large population of small perturbations of the baseline which rarely exceed 1-2 mm and do not vary with pellet size. The second is made up of much larger, regularly spaced gapes whose amplitude varies directly with pellet size. To examine the temporal organization of mandibulation in greater detail we computed frequency distributions of intermandibulation intervals for each subject. Because the individual distributions were similar the data were combined and the data for four birds is presented in Figure 22. The figure confirms the fact that for all pellet sizes intermandibulation intervals show a consistent peak at 80 ms. As we move towards the larger target sizes a second group of intervals becomes evident with shorter and more variable intervals.

DISCUSSION

Relation between gape and amplitude of jaw opening movements

The relationship between gape and amplitude for each of the movement classes is shown in Figure 23. As noted earlier, Peak Gape = Initial Gape + Amplitude. If initial gape is a constant (i.e., does not vary with pellet size) one would predict that Peak Gape for three of the four movement classes (Grasps, Prepecks, Swallows) will differ from Peak Amplitude by some constant value. During mandibulation, however, there is a pellet between the beaks so that the jaw opening movement takes off from an existing initial gape determined by the pellet size. Thus for mandibulation the formula becomes Peak Gape = Pellet Size + Amplitude. The difference between any two corresponding data points on the functions for mandibulation shown in Figure 23 (lower right quadrant) represents almost exactly the pellet size for that point.

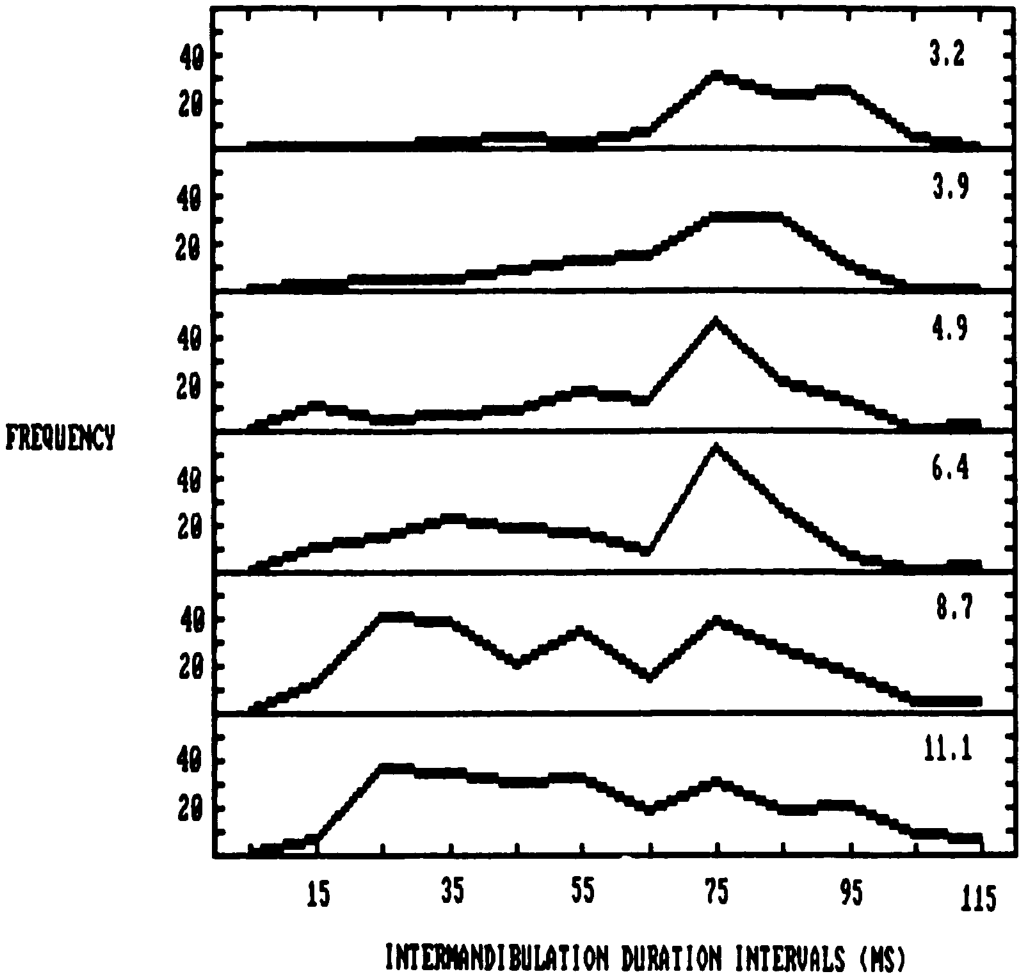


Figure 22: Frequency distributions of intermandibulation intervals with respect to target size. The plots are average of four of the subjects, reflecting a similar trend for each single subject

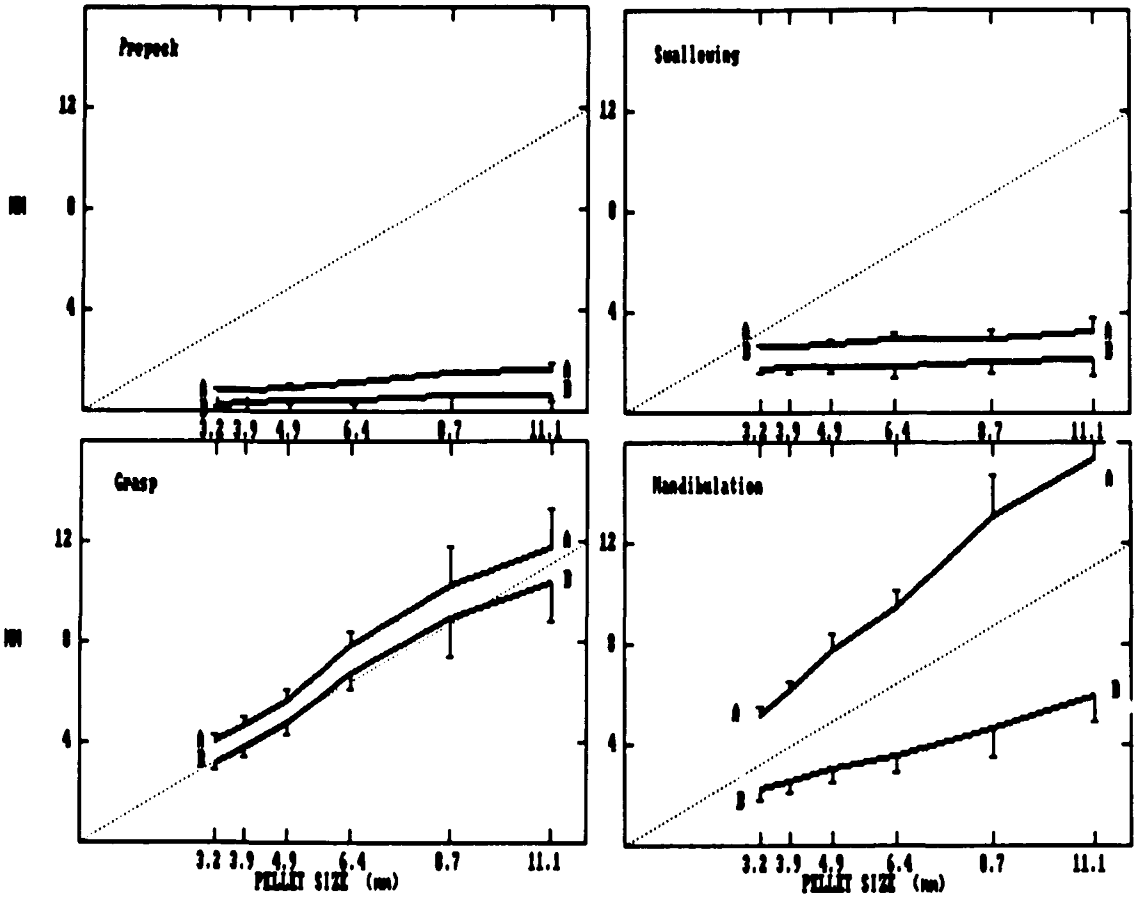


Figure 23: Peak gape (A) and peak amplitude (B) functions related to pellet size for all four gape classes. Mean values were taken from all the six birds. Vertical lines over each one represent standard errors of the mean.

Grasping

The scaling of opening amplitude to pellet size approximates a linear function over most of the range of target sizes. (Pigeons appear to have considerable difficulty dealing with the 11.1 mm pellets. In all cases some motor learning appears necessary to make their ingestion possible and they may lie outside the normal size range of food objects). The existence of a systematic relationship between gape and target size has been reported in several previous studies (Zeigler, et al.,1980; LaMon and Zeigler, 1984; Deich, et al.,1985). All these reports have noted that gape size for any pellet size is slightly larger than target size and have interpreted this observation as an "overshoot" by the bird. Such a systematic overshoot could be of functional utility in minimizing the chances that the seed would be struck (and deflected away) by the upper beak (Bock, 1964). However no such "overshoot" was evident in the present findings since opening amplitude was found to be rather precisely scaled to target size. The difference in results reflects the difference between gape and amplitude measures of jaw opening. This conclusion does not negate the "observation" of an overshoot but indicates that it results from a combination of initial gape and actual jaw displacement. Given the possible functional utility of the achieved overshoot, it might even be argued that the bird utilizes information as to initial gape in scaling the amplitude of the grasp. (A comparable argument will be made for the control of opening amplitude during mandibulation, see below).

The fact that scaling functions for Successful and Unsuccessful grasps are almost identical suggests first, that the failure of an Unsuccessful grasp is not due to an error in the control of jaw opening but is more likely to involve a failure in peck localization. For example, in the present study the spherical pellets may still be moving within the watch glass, making them more difficult pecking targets.

The precision with which jaw-opening movements are scaled to target size during grasping is impressive. For most subjects a shift in target size greater than about 1.0 mm elicits a significant shift in opening amplitude. These findings are consistent with those of a recent study of size-difference thresholds in the pigeon (Hodos, Weiss and Bessette, 1986). Using a series of projected visual stimuli (3-15 mm) which closely approximates the range used in the present study these workers found that pigeons are very sensitive to small differences in the size of projected visual stimuli (mean threshold = 0.80 mm) and that the average pigeon could fractionate the stimulus continuum into approximately six discriminable units.

Mandibulation

As with grasping, jaw opening amplitude during mandibulation is adjusted to stimulus size. The shift in the distribution of amplitudes parallel to pellet size is not as clear as for grasping (Figure 10). This is probably related to an increase in the amplitude ranges during mandibulation.

Although opening amplitudes during mandibulation are scaled to target sizes (Table 2 and Figures 11 and 12) the slope of the scaling function is less than that seen in grasping. As Figure 23 indicates, opening amplitudes vary over a significantly smaller range and opening gapes show a substantial overshoot by comparison with grasping.

These differences are related to the different tasks required of the bird during grasping and mandibulation. During grasping, the pigeon's task is to produce an opening amplitude exactly scaled to target size. However, during mandibulation, the pigeon's task is to move a target from the beak tip to the back of the mouth by a series of combined head and jaw movements. Since there is already a pellet within the mouth, generation of an opening movement directly scaled to pellet size would produce an overshoot in final gape equal to the pellet size. For some pellets this would require an abnormal degree of jaw opening. Alternatively, opening amplitude could be maintained at some constant value independent of pellet size. As Figure 23 and Table 5 indicate, neither of these strategies is used during mandibulation.

By comparison of the gape and amplitude functions in the lower right hand quadrant (Fig. 23), it is clear that jaw opening varies with pellet size such that the opening amplitude differs from opening gape by an amount equal to initial gape (i.e. approximately pellet size). The predicted value for initial gape (= the pellet size) and the obtained values are presented in Table 5 and are in good agreement. The lack of agreement probably represents the fact that pellets are not always centered precisely between the beaks during the initial gape. This observation clearly implies that the bird is using information about initial gape (including pellet size) to control opening amplitude.

Table 5: Starting gape, peak amplitude, and peak gape mean values for all six pellet sizes during mandibulation. Mean values are the result of all six birds combined. Numbers in parenthesis represent standard deviations. (I.G.=Initial Gape; P.A.=Peak Amplitude; T.S.=Target Size).

	Target Size					
Variable	3.2	3.9	4.9	6.4	8.7	11.1
Initial Gape	2.93 (.23)	3.59 (.51)	4.69 (.70)	5.98 (.96)	8.27 (1.83)	9.32 (2.55)
Peak Amplitude	2.21 (.71)	2.51 (.79)	3.01 (.98)	3.44 (1.31)	4.49 (1.97)	5.81 (2.96)
Recorded Gape (I.G.+ P.A.)	5.14 (.79)	6.10 (.99)	7.69 (1.27)	9.42 (1.55)	12.76) (2.67)	15.13 (3.37)
Predicted Gape (I.G + T.S.)	6.13	7.49	9.59	12.38	16.97	20.42

There are two possible sources of information as to initial gape; proprioceptive input about jaw position, and tactile inputs produced by contact of the pellet with the oral surfaces of the upper and lower beaks. Electrophysiological analyses of trigeminal sensory structures in the pigeon (Zeigler and Witkovsky, 1968; Silver and Witkovsky, 1973) have shown that both types of inputs are available at the level of the brainstem trigeminal complex (Main Sensory Nucleus, Spinal Trigeminal Nucleus).

Prepecks

The analysis of prepeck movements shows some scaling of amplitudes to target size, but it is not consistent for all the birds. However, there is a systematic temporal relation between the occurrence of prepecks and grasps. As the data in Figure 16 indicate, prepeck onset occurs about 180 ms prior to the onset of the next grasp response and its duration is about 75 ms. These data are of interest in the light of certain observations as to the spatio-temporal organization of the pigeon's pecking behavior.

Goodale (1983) has shown that during pecking at food the pigeon makes two distinct successive fixations (F1 and F2), each of which is followed by a period of head descent. According to Goodale, birds make the decision to peck (for consummatory pecks) during a head fixation (F1) that lasts 220 ms. A second fixation (F2) follows the first one, with a duration of 96 ms. Between these two fixations there is a saccadic head movement that lasts an average of 84 ms, at the same time that the head moves down until it stops during F2. After F2 the head moves down again for approximately 72 ms until it grasps the seed. The beak begins to open 23-35 ms after the begining of the movement towards the seed. These two sets of time events are related (Figure 24) in such a way that the occurrence of prepecks correlates very closely with the head movement between fixations in Goodale's study.

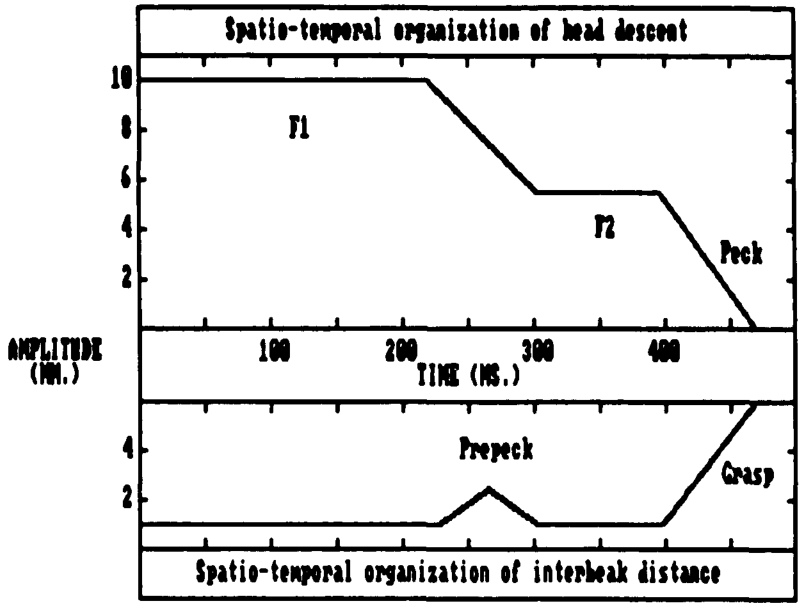


Figure 24: Spatiotemporal organization of head descent (Goodale) to show its correspondence with prepeck movements.

Given these observations, prepecks may reflect the acceleration and/or deceleration phases from F1 to F2 passively producing this small beak movement. Goodale's study also reports that from F1 to F2 there is a change in the orientation of the beak's axis with respect to the seed. This change in orientation could produce movements of the beaks relative to each other, which is recorded as a prepeck by the Hall-effect system. Alternatively prepeck could reflect activity in the protractor muscle which serves to "unblock" the mandible (Zweers, personal communication, 1985). The analysis provides no support for the hypothesis that prepecks are sensitive to target size and could serve a "presetting" function for the grasps which they precede.

Swallows

This analysis provides no evidence for a systematic scaling of amplitude to pellet size for swallowing movements. As with prepecks, these movements may be passively produced and reflect activity in other portions of the oromotor system.

Thus, of the four movement classes discussed in this part, only two, grasping and mandibulation, involve a systematic scaling of jaw movement amplitude to target size. Prepecks and swallows, although show some correlation for some birds, they are not scaled in the same consistent way.

PART II: KINEMATICS OF GRASPING AND MANDIBULATION

INTRODUCTION

The accurate adjustment of movement amplitude to task requirements (response scaling) is an important function of motor control mechanisms. In Part I it was demonstrated that the amplitude of jaw-opening movements during some prehensile behaviors in the pigeon is scaled to target size. The movements involved are extremely rapid (grasp: 60-80 ms; mandibulation: 30-50 ms) and are unlikely to be under the control of peripheral feedback during their execution. In these respects they may be considered as simple behavioral models of amplitude scaling, analogous to the tasks used in many studies of human motor control. Moreover, the relative simplicity of the effector system involved (the jaw) and the ease with which the behaviors may be elicited suggests that the pigeon could provide an excellent preparation for neurophysiological studies of motor control mechanisms.

An important starting point for such studies is the identification of kinematic variables which are controlled to produce the scaled outputs characteristic of the behavior. This Part II was designed to determine the trajectories of jaw-opening movements during grasping and mandibulation and their relation to a number of putative controlling variables including peak velocity, peak acceleration and rise times. The relationships among these kinematic variables were then examined in order to specify the putative motor control "strategies" which may account for such scaling. Finally, the kinematic data were analyzed to determine the extent to which movement trajectories are subject to corrective adjustments during their execution.

In order to characterize the motor control strategy underlying the grasping and mandibulation movements of the pigeon, a kinematic analysis of the movement trajectories associated with these behaviors was carried out. Such an analysis involved the measurement of the critical kinematic variables related to it. A movement, such as the pigeon's jaw opening, could be characterized by a sigmoidal function (Figure 25),which is defined by a maximum point (equivalent to **peak amplitude**), a minimum point (equivalent to **initial gape**), and an inflection point (or **peak velocity** of the trajectory) between the two previous points.

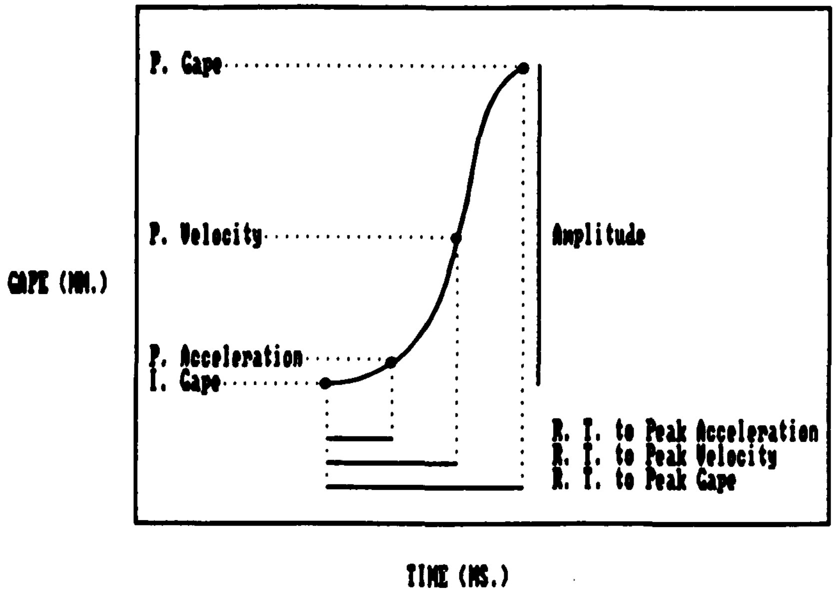


Figure 25: Schematic diagram of parameters describing the kinematics of and idealized jaw opening movement.

In such a sigmoidal function, peak amplitude is determined by peak velocity. At the same time, an earlier measure (**peak acceleration**) determines the peak velocity of the trajectory, and consequently, influencing also peak amplitude. These variables are illustrated schematically in Figure 25, representing an idealized opening trajectory. The time frames associated with each of the above kinematic variables are also represented on the diagram.

METHODS

To determine which of the two pulse-step strategies (see General Introduction) accounted for the amplitude scaling characteristic of the movements, we examined the relation between target size and each of the kinematic variables as well as the relations among the kinematic variables themselves.

The kinematic analysis was based upon a minimum of 10 movement trajectories for each target size and subject. In the first stage of the analysis the peak opening amplitude and its first and second derivatives (peak opening velocity and acceleration) were computed off-line for each trajectory as were the rise times to each of these peaks. Functions relating target size to each of these variables were then plotted and the data were subjected to a statistical analysis employing analysis of variance and correlation procedures. Interactions among the kinematic variables were examined using partial correlation techniques. In the second stage of the analysis a series of multiple correlation analyses were carried out to assess the extent to which jaw-opening trajectories are subject to compensatory correction during their execution. The first part of the analysis was carried out on unsmoothed data. The data used for the second stage of the analysis was smoothed twice, each time by applying a three-point running average. (A more extensive discussion about the subject, and the motives to choose two degrees of smoothing, can be seen on Appendix A).

The analysis was applied to gapes associated with successful grasp and mandibulation movements. Initial gape, peak amplitude, and rise times were obtained directly from scored raw data. Peak velocity was obtained as the highest instantaneous velocity along the movement trajectory (from the initial gape up to the peak amplitude). Peak acceleration was obtained as the greater instantaneous acceleration from the initial gape up to the peak velocity point.

RESULTS

Grasping

Relation between kinematic variables and target size.

Figure 26 presents jaw opening trajectories associated with grasping behavior for a single representative subject to illustrate the relation between movement amplitude and its first and second derivatives. Curves are arranged from top to bottom in descending order from the largest to the smallest target size. Curves on the right hand side are normalized with respect to the highest values on the left hand side. As was pointed out in Part I, the amplitude trajectories are scaled to target size and this is also the case for peak velocity and peak acceleration. The normalized data suggest some degree of similarity on the profiles.

In Figure 27 the same trajectories are aligned with respect to the starting point and those on the right are normalized as before. The data suggest some degree of scaling of both amplitude and duration with respect to pellet size.

The extent of this scaling was determined for each of the kinematic variables by plotting functions relating these kinematic variables to pellet size. In Figure 28 amplitude, velocity and acceleration data for a single subject (F8460) are compared with their respective rise times. Averaged functions for all six birds are presented in Figure 29, while Table 6 presents correlation coefficients and F tests associated with these analyses for each of the birds.

For both the individual and group data amplitude, velocity and acceleration tend to be linear functions of pellet size and the correlation coefficients for each function are significant beyond the 0.001 level (Table 6). For the rise time measures the associated correlation coefficients though significant tend to be considerably smaller. Note that for velocity and acceleration all correlations are significant ($p < .001$) but this is not the case for the duration measures.

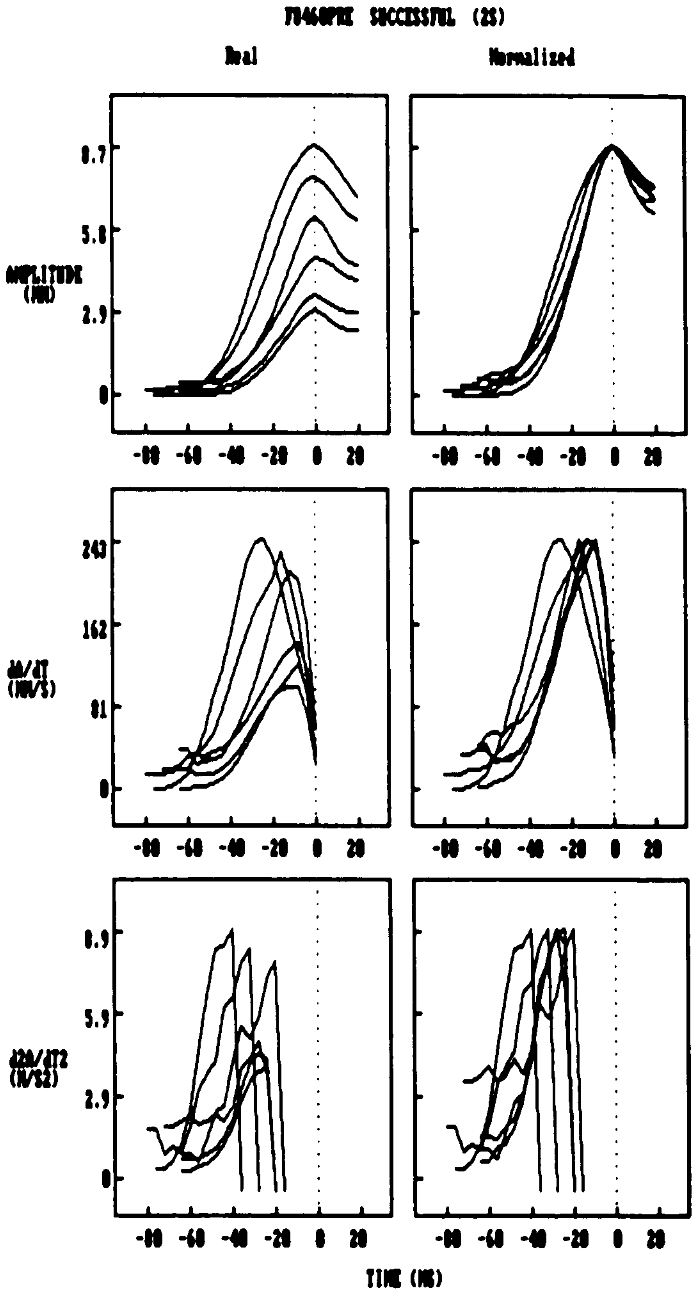
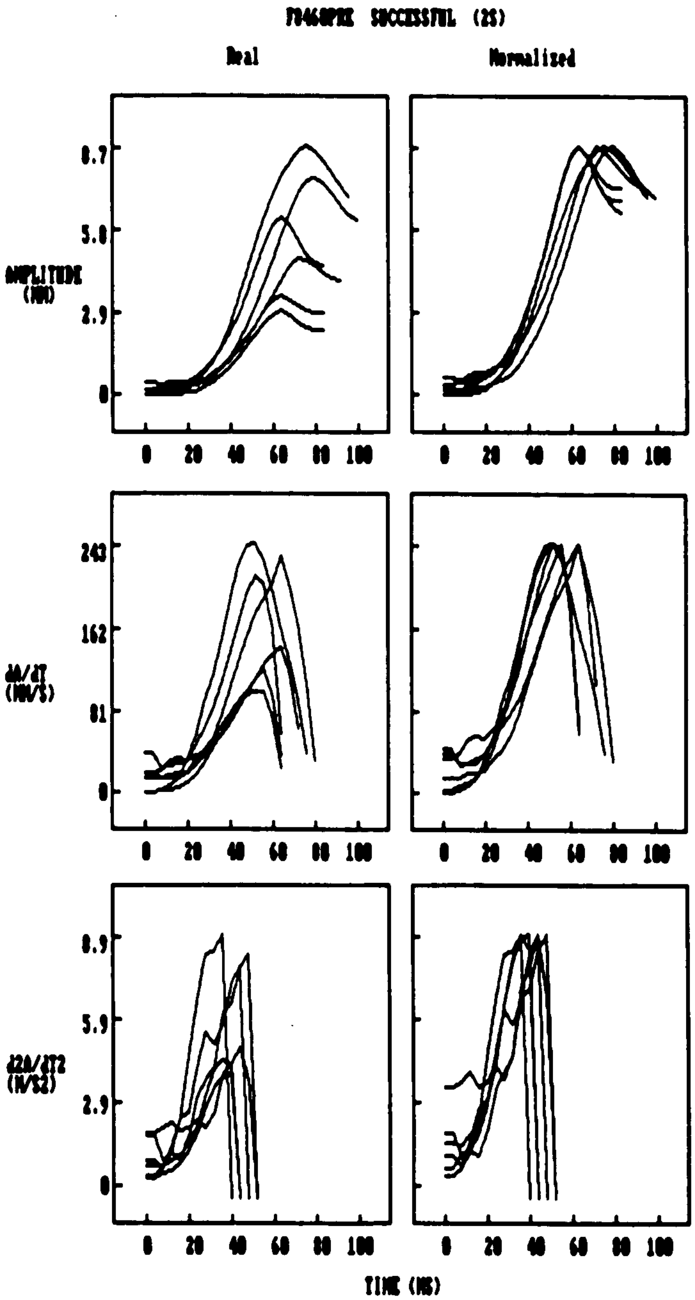


Figure 26: Jaw opening trajectories for target amplitude, and its first and second derivatives across all six pellet sizes. Figures on the right hand side are normalized with respect to the highest values on figures on the left hand side. Trajectories are aligned with respect to the peak gape.



<u>**Figure 27**</u>: Jaw opening trajectories for target amplitude, and its first and second derivatives across all six pellet sizes. Figures on the right hand side are normalized with respect to the highest values on figures on the left hand side. Trajectories are aligned with respect to the point of initial gape.

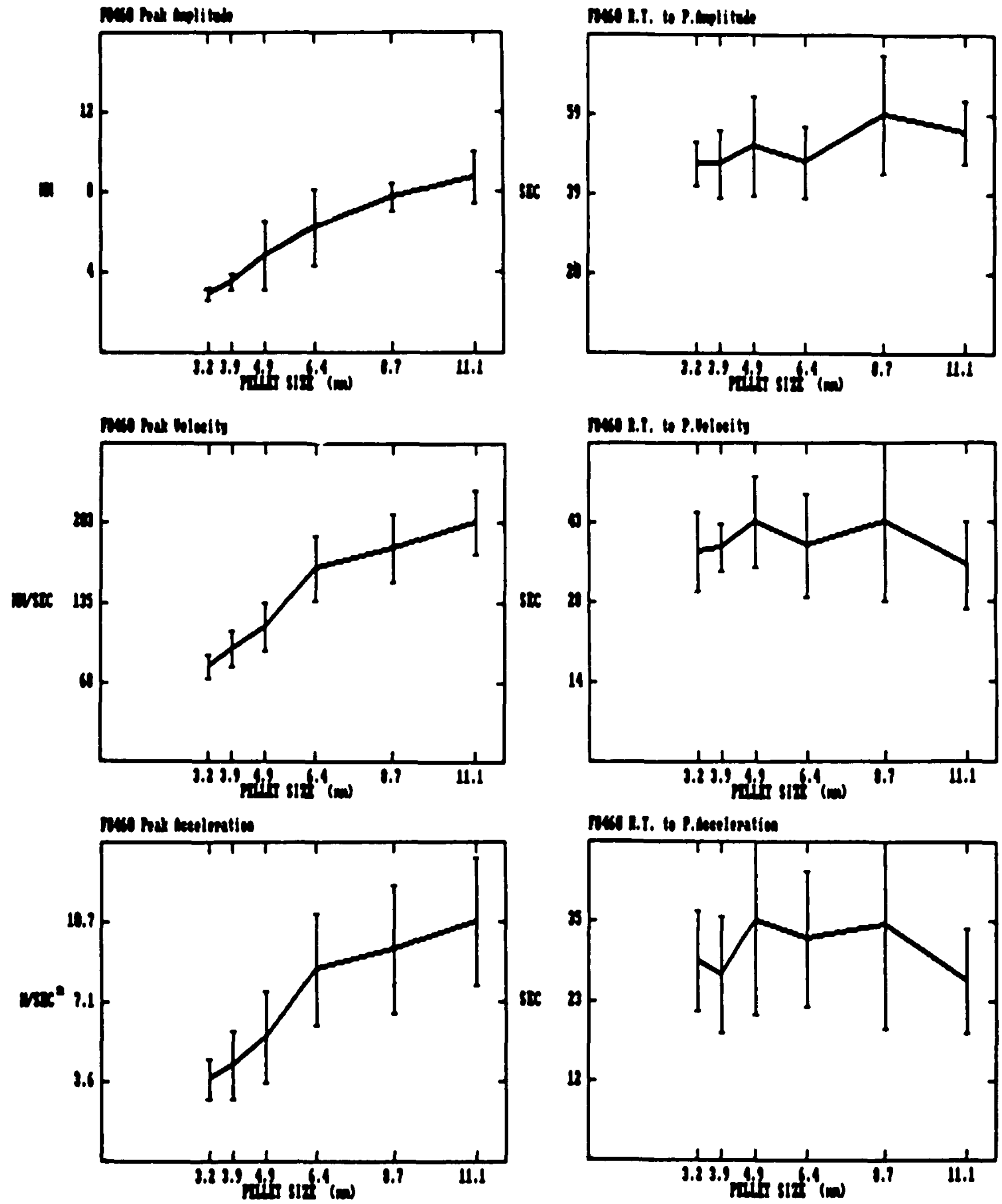


__Figure 28__: Functions relating target size to amplitude, and its first and second derivatives (left hand side), as well as the functions relating target size with duration measures (right hand side), for a single bird (F8460).

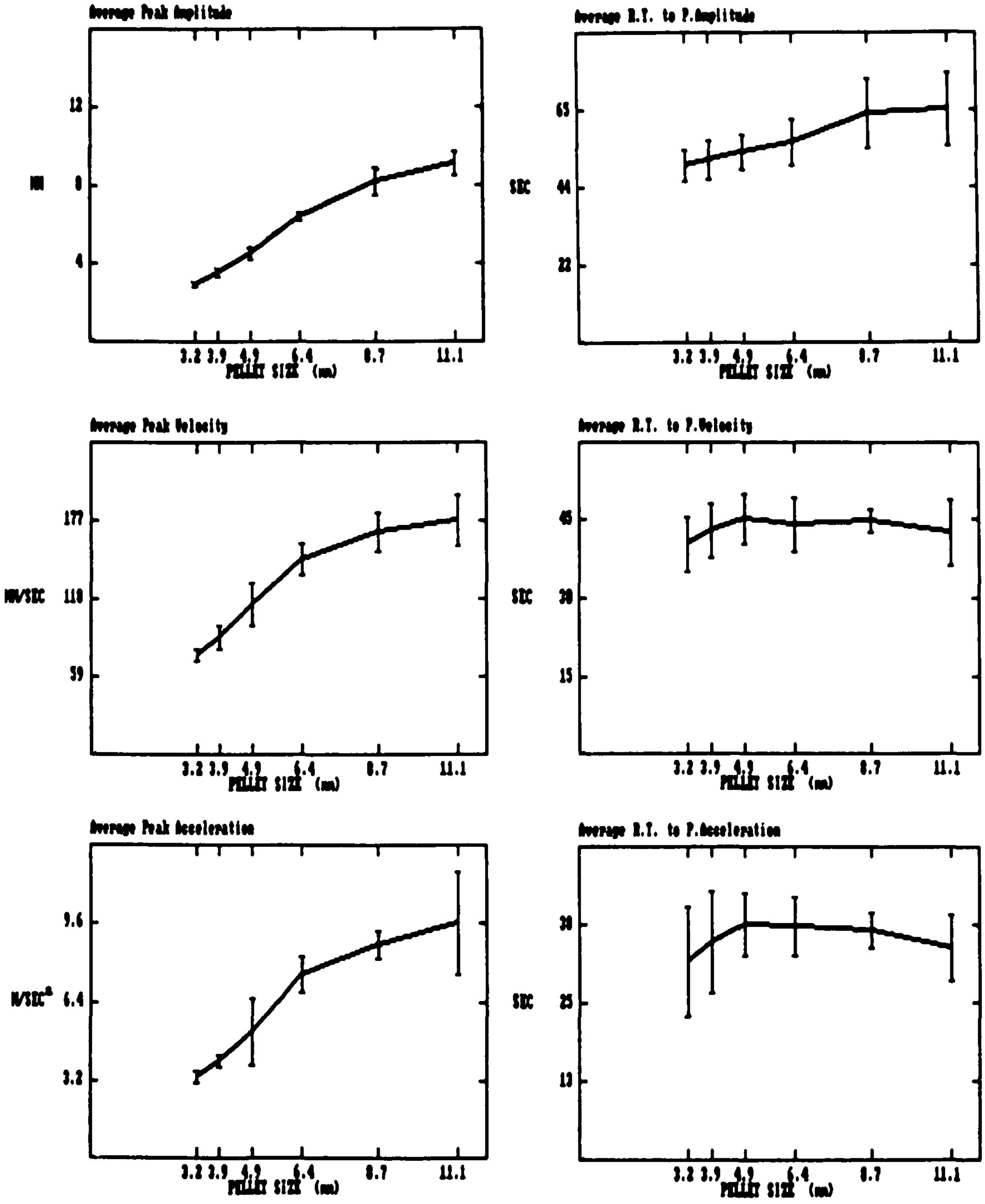


Figure 29: Functions relating target size to amplitude, and its first and second derivative (left hand side), as well as the functions relating target size with duration measures (right hand side). Plots are average of all six birds.

Table 6: Correlations and anovas for amplitude, first and second derivative, and their respective rise times, with target size, during grasping. (*:p <.01; **:p <.001)

Variable		Bird					
		F8452	F8455	F8459	F8460	F8479	F8491
Amplitude	r	.88 **	.84 **	.85 **	.86 **	.93 **	.87 **
	F	59 **	55 **	32 **	40 **	99 **	49 **
Peak Velocity	r	.72 **	.74 **	.65 **	.87 **	.81 **	.75 **
	F	24 **	27 **	10 **	52 **	47 **	18 **
Peak Accelerat.	r	.51 **	.59 **	.47 **	.76 **	.80 **	.65 **
	F	6.3**	12 **	5.0**	20 **	41 **	10 **
R.T. P.Amplit.	r	.35 *	.32 *	.70 **	.33 *	.81 **	.60 **
	F	3.7*	3.0	14 **	2.6	34 **	8.8**
R.T. P.Veloc.	r	-.22	.14	.77 **	-.04	.40 **	.54 **
	F	1.3	1.6	20 **	1.2	5.1**	6.3**
R.T. P.Accel.	r	-.29 *	-.04	.51 **	-.01	.53 **	.49 **
	F	2.4	.92	5.1**	1.3	11 **	4.5*

Relations among kinematic variables.

In order to provide data bearing on the bird's motor control strategy we examined the relations among these kinematic variables. Figure 30 illustrates these relations for a single subject. For each pair of kinematic variables, the regression lines within and between target sizes are plotted as well as their associated correlation coefficients. Peak amplitude is significantly correlated with both peak velocity and rise time, but the correlation with the rise time is considerably lower. The same trend is evident in the data of the six individual subjects presented in Table 7.

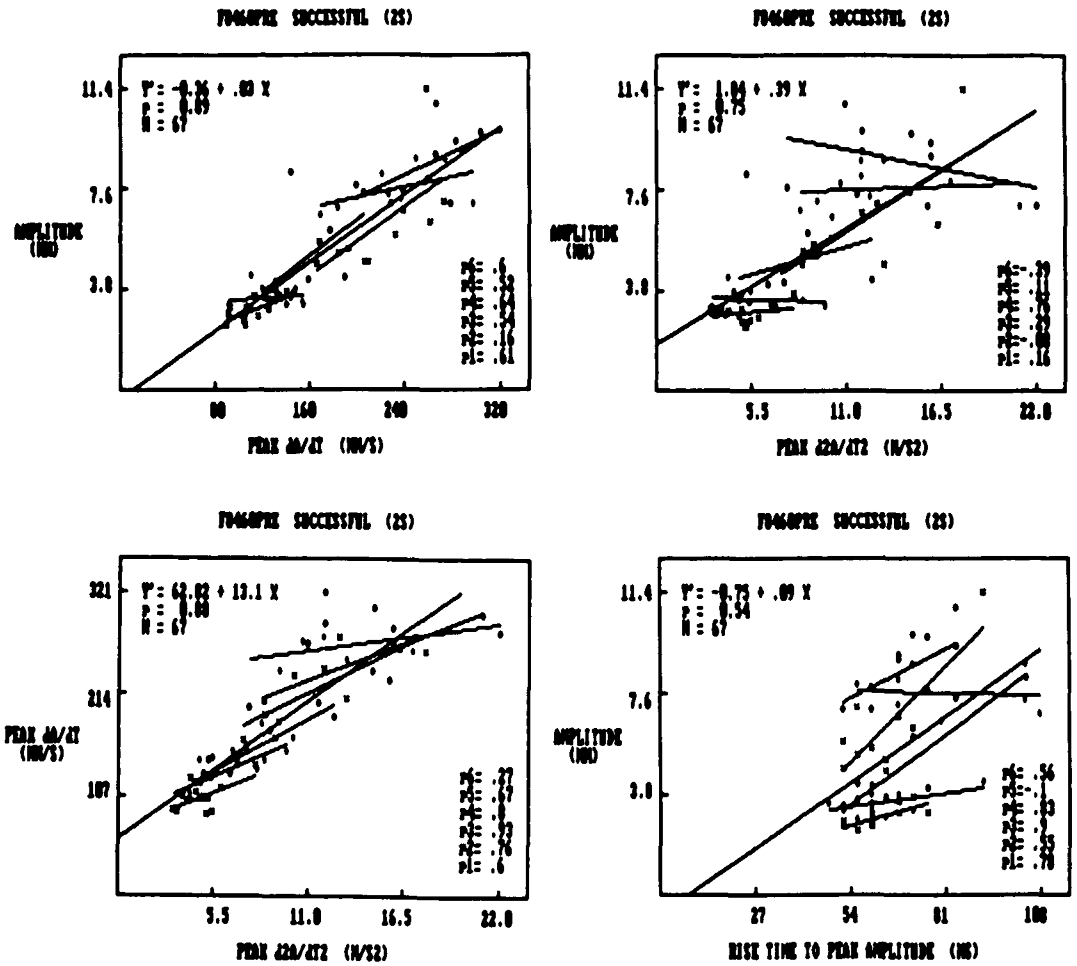


Figure 30: Regression line and correlation coefficients between kinematic variables and peak amplitude for successful grasps. For each plot, the line that crosses the coordinate axis is the regression line across all target sizes. Shorter lines represent regression lines for each pellet size independently (lowest, small target; highest, large target). Bottom right hand side of each plot represents correlation coefficients for each particular pellet size (r1 for the smallest, and r6 for the largest target). Correlation, equation of the regression line, and number of data points used (N) are represented on the upper left corner of each plot.

Table 7: Correlations among kinematic variables during grasping. (*: p <.01; **: p <.001).

	Bird					
Variables	F8452	F8455	F8459	F8460	F8479	F8491
P.Velo-P.Ampl.	.86 **	.92 **	.89 **	.89 **	.84 **	.92 **
P.Acce-P.Ampl.	.64 **	.76 **	.77 **	.75 **	.84 **	.79 **
P.Acce-P.Velo.	.72 **	.84 **	.93 **	.88 **	.90 **	.93 **
RTPAm.-P.Ampl.	.45 **	.44 **	.76 **	.54 **	.91 **	.59 **
RTPVe.-P.Ampl.	-.03	.27	.81 **	.19	.45 **	.62 **
RTPAc.-P.Ampl.	-.11	.17	.68 **	.21	.54 **	.58 **

Correlations between rise time and peak amplitude, though significant, are considerable lower. Furthermore, the other rise time measures are significant for only three of the subjects. The data presented above indicates that peak velocity accounts for most of the variance in peak amplitude, but that control of rise time also makes some contribution to the scaling of grasping movements.

To clarify that contribution it may be helpful to recall the two alternative models proposed to account for the control of peak amplitude. Both models imply that target size will control peak amplitude but differ with respect to the pathway presumed to mediate that control. As it was shown, peak amplitude is correlated with both pellet size and peak velocity, while pellet size is also correlated with peak velocity. A similar relationship holds for target size with respect to both rise time and peak amplitude. These relationships are expressed schematically in the diagram below (Figure 31). Under a pulse-height strategy, for instance, peak amplitude is accomplished through some actual peak velocity achieved during the movement (path from peak velocity to peak amplitude). At the same time, the stimulus (target size) demands from the nervous system some required peak velocity to produce the appropriate peak amplitude (path from target size to peak velocity). The same could be explained under a pulse-width strategy (bottom half of the diagram). To assess the independent contributions of each of the kinematic variables within each model, partial correlations were computed, that is, correlations among each pair of variables were computed while holding the third variable constant. The results of this analysis are presented in Table 8.

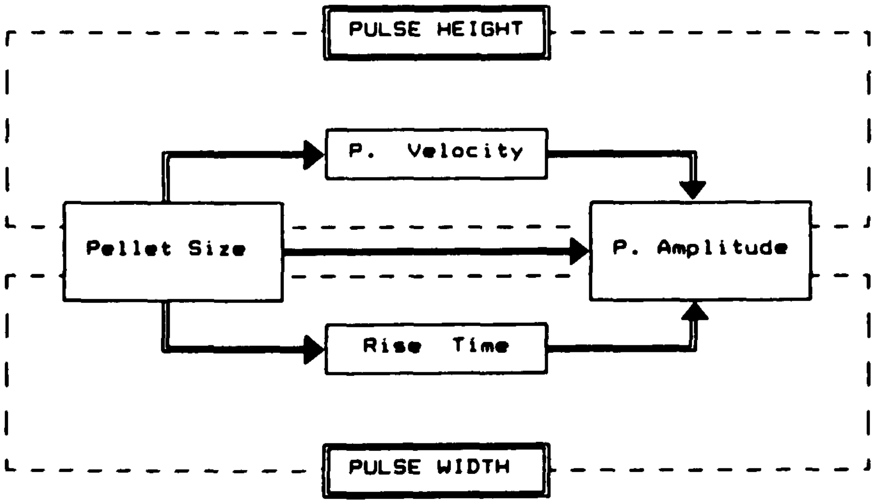


Figure 31: Diagram representing the pathways involved under a pulse-height and a pulse-width control strategies.

Under a pulse height strategy (Table 8, upper half) peak velocity and target size account equally for the variance in peak amplitude. Under a pulse width strategy (Table 8, lower half) target size accounts for twice as much of the variance in peak amplitude, although both correlations are significant. These data indicate that target size accounts for a significant proportion of the variance in peak amplitude independent of the operation of either rise time or peak velocity and that it explains more of the variance under a pulse-width than under a pulse-height model.

The analyses up to this point do not permit to distinguish quantitatively between the contributions of rise time and velocity variables to the control of peak amplitude. That is, peak amplitude appears to involve a complex interaction among rise time, peak velocity and target size. To explore the nature of that interaction, a series of second order partial correlations were carried out between pairs of variables while holding the other two variables constant (Table 9).

The data in Table 9 confirm the fact that target size, peak velocity and rise time variables contribute (in different degrees) to the control of amplitude. They also indicate a strong negative correlation between peak velocity and rise time.

Table 8: Partial correlations, during grasping, between two kinematic variables holding the third one constant. Data values were obtained after two degrees of smoothing. Mean values were computed using Fisher's Z transformation. (TS=Target Size; PA=Peak Amplitude; PV=Peak Velocity; RT=Rise Time to Peak Amplitude; Comp.=variables compared; Cont.=variable controlled. *: p <.01; **: p <.001).)

Variables	**Bird**						
Comp./Cont.	F8491	F8479	F8460	F8459	F8455	F8452	**Mean**
TS-PA/PV	.69**	.78**	.38**	.78**	.60**	.74**	**.68****
PV-PA/TS	.82**	.40**	.56**	.84**	.82**	.67**	**.71****
TS-PV/PA	-.26	.14	.45**	-.44**	-.15	-.15	**-.07**
TS-PA/RT	.80**	.79**	.86**	.68**	.82**	.86**	**.81****
RT-PA/TS	.17	.73**	.53**	.44**	.33*	.32*	**.44****
TS-RT/PA	.21	-.24	-.31*	.16	-.10	-.11	**-.07**

Table 9: Partial correlations, during grasping, between two kinematic variables holding the other two constant. Second-order partial correlations were computed upon the first-order partial correlations. Legend as in table 8.

Variables	**Bird**						
Comp./Cont.	F8491	F8479	F8460	F8459	F8455	F8452	**Mean**
TS-PA/PV-RT	.51**	.60**	.28	.68**	.60**	.70**	**.58****
PV-PA/TS-RT	.89**	.64**	.75**	.86**	.85**	.81**	**.81****
RT-PA/TS-PV	.61**	.82**	.73**	.52**	.53**	.64**	**.66****
TS-PV/PA-RT	-.16	.02	.34*	-.42**	-.22	-.27	**-.13**
PV-RT/TS-PA	-.62**	-.54**	-.60**	-.36*	-.43**	-.61**	**-.54****
TS-RT/PA-PV	.07	-.19	-.03	-.02	-.18	-.25	**-.11**

A number of conclusions emerge from the analyses.

1) Peak velocity is well scaled to target size and predictive of peak amplitude. However, as the data in Table 8 show, peak velocity did not account for all the variance in peak amplitude (variance unaccounted for = $1-r^2$), oscillating between 16% and 27%.

2) An early measure of peak velocity, peak acceleration (with which it shares a highly significant correlation shown also in Table 7), was both highly predictive of the peak amplitude achieved and scaled to the target amplitude. That means that, to some extent, critical parameters of the peak amplitude have been planned before the response initiation.

3) The initial movement trajectories differed from perfect scaling to target size, that is, target size did not account for all the variance in peak acceleration leaving unexplained from 36% to 78% of the variance in peak acceleration (obtained from Table 6).

4) As Gordon (1985) has pointed out, differences between trajectory dynamics required to achieve a particular target size and the trajectory dynamics actually emitted could be thought of as errors. To the extent that the actual peak velocity does not match the peak velocity required by target size the actual amplitude would differ from the required amplitude in either the positive or negative direction (overshoot, undershoot). In such a situation, error correction would require an adjustment of the final trajectory so as to compensate for such errors.

Gordon has characterized such adjustments as reflecting a process of "current control" , and has developed an analytical strategy for assessing the contribution of this process to the scaling of movement trajectories. The current control hypothesis may be tested by comparing the contribution of the two pathways involved in each of the pulse-step models. For the pulse height model, target size may influence peak amplitude either directly, or indirectly through its action upon peak velocity. The combined action of these two steps can be computed by means of a multiple regression, where $R^2_{y.1,2}$ would represent an estimate of the proportion of the variation of peak amplitude jointly explained by target size and peak velocity. When we subtract this value from $r^2_{y.1}$, which represents the percentage of variance accounted for solely by the influence of peak velocity upon peak amplitude, then we can obtain a measure of the increased variance accounted for by the corrective effect of target size.

Such an analysis was applied to the grasping data and the results are presented in Figure 32, which shows that for all birds, the combined effect of target size and peak velocity explains more of the variance in peak amplitude than peak velocity alone. Table 10 indicates that the percentage of variance accounted for solely by peak velocity varied from 70% to 85% (mean across birds= 78%), and the increment introduced by the corrective effect of pellet size varied from 3% to 19% (mean across birds= 10%), being significant for all six subjects

Table 10: Percentage of variance in peak amplitude, during grasp, accounted for by peak velocity ($r^2_{y.1}$), and by the joint action of peak velocity and target size ($R^2_{y.1,2}$). The difference between the two of them represents the corrective effect of target size. Significance of the difference was tested by the F test of significance in multiple regression. (*: p <.01; **: p <.001).

	Bird					
Regression	F8491	F8479	F8460	F8459	F8455	F8452
$r^2_{y.1}$	85	70	79	79	85	74
$R^2_{y.1,2}$	92	89	82	92	90	88
$R^2_{y.1,2} - r^2_{y.1}$	7 **	19 **	3 **	13 **	5 **	14 **

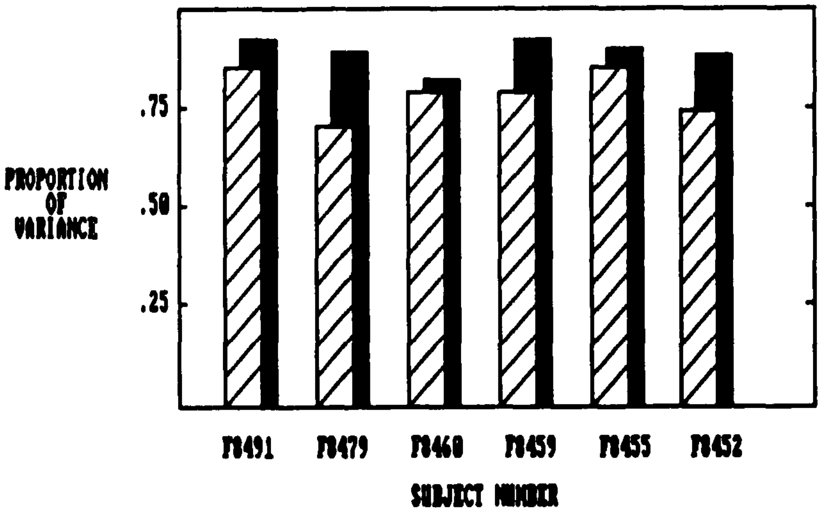


Figure 32: Proportion of variance in peak amplitude, during grasp, accounted for by peak velocity ($r^2_{y.1}$, dashed bars), and by the joint effect of peak velocity and target size ($R^2_{y.1,2}$, dark bars). The difference between the two bars represents the corrective effect of pellet size. Data are showed in table 10, where the significance of the corrective effect is also represented, computed by the F test of significance in multiple regression (*: p<.01, **: p<.001).

The same analysis applied to the pathways involved under pulse width (as shown in Figure 33 and Table 11), shows that for four out of the six birds, the corrective effect explained more variance in peak amplitude than rise time did. The percentage of variance accounted for by rise time varied from 11% to 83% (mean across birds= 36%), while the corrective effect added from 11% to 68% (mean across all birds= 44%), being significant for all birds (F test, p<.001).

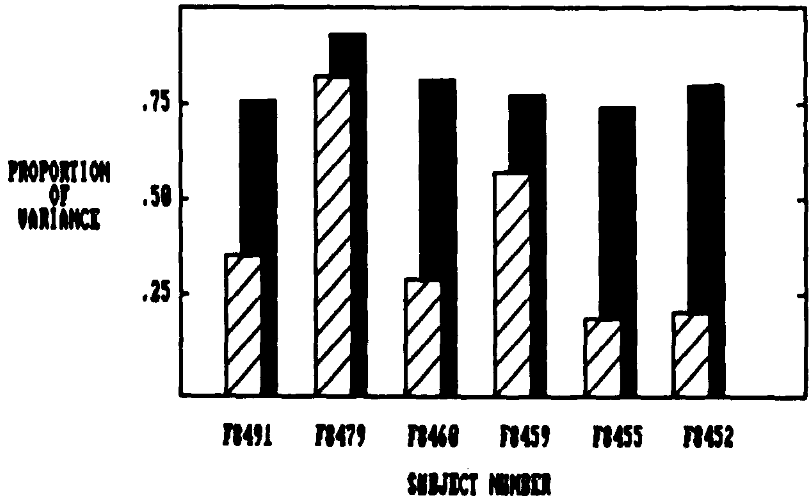


Figure 33: Proportion of variance in peak amplitude, during grasping, accounted for by rise time to peak amplitude ($r^2_{y.1}$, dashed bars), and by the joint effect of rise time and target size ($R^2_{y.1,2}$, dark bars). The difference between the two bars represents the corrective effect of pellet size. Legend as in Figure 32.

Table 11: Percentage of variance in peak amplitude, during grasping, accounted for by rise time to peak amplitude ($r^2_{y.1}$), by the joint action of rise time to peak amplitude and target size ($R^2_{y.1,2}$), and the difference between the two of them (to show the corrective effect: positive or negative errors). Legend as in Table 11.

	Bird					
Regression	F8491	F8479	F8460	F8459	F8455	F8452
$r^2_{y.1}$	35	82	29	57	19	20
$R^2_{y.1,2}$	76	93	81	77	74	79
$R^2_{y.1,2} - r^2_{y.1}$	41 **	11 **	52 **	20 **	54 **	59 **

The partial correlation between target size and peak amplitude when the effect of peak velocity was removed, is equivalent to the correlation between the error in the initial trajectory and the variance in peak amplitude that is not explained by peak velocity. So, using the partial correlations from Table 8, we can see that the compensatory adjustments to the trajectory explain from 15% to 60% (mean= 46%) of the variance not explained by pulse height control.

What are these compensatory adjustments based upon?. A reasonable way to explain it is by looking at a possible contribution of the other main variable involved in the process, that is, rise time. If rise time is added to the regression equation predicting peak amplitude after peak velocity has first been used, then the proportion of variance in peak amplitude explained by the combined action of the two variables increases significantly as it was shown in Table 9. By comparing this table with Table 11, it is possible to see that the variance explained by target size (corrective effect) is very similar to that explained by rise time in both cases after the effect of peak amplitude was counted first. This comparison suggests that the corrective or compensatory effect of target size is made through rise time.

If peak velocity accounts for most of the variance in peak amplitude, and rise time adds some contribution, it might be expected some relationship between them. To assess this relation, correlations between peak velocity and rise time to peak amplitude were computed for each of subjects and each of the target sizes (to increase sample sizes for this analysis we pooled the data for both successful and unsuccessful grasps). As Table 12 shows, 80% of the correlations are negative (29 out of 36). Only 13 of these are significant, probably because of the small number of gapes in the sample (approximately 20 for every target size). The relationships between peak velocity and rise time to peak amplitude are plotted, for each of the subjects, in Figure 34, which shows regression lines within and across target sizes.

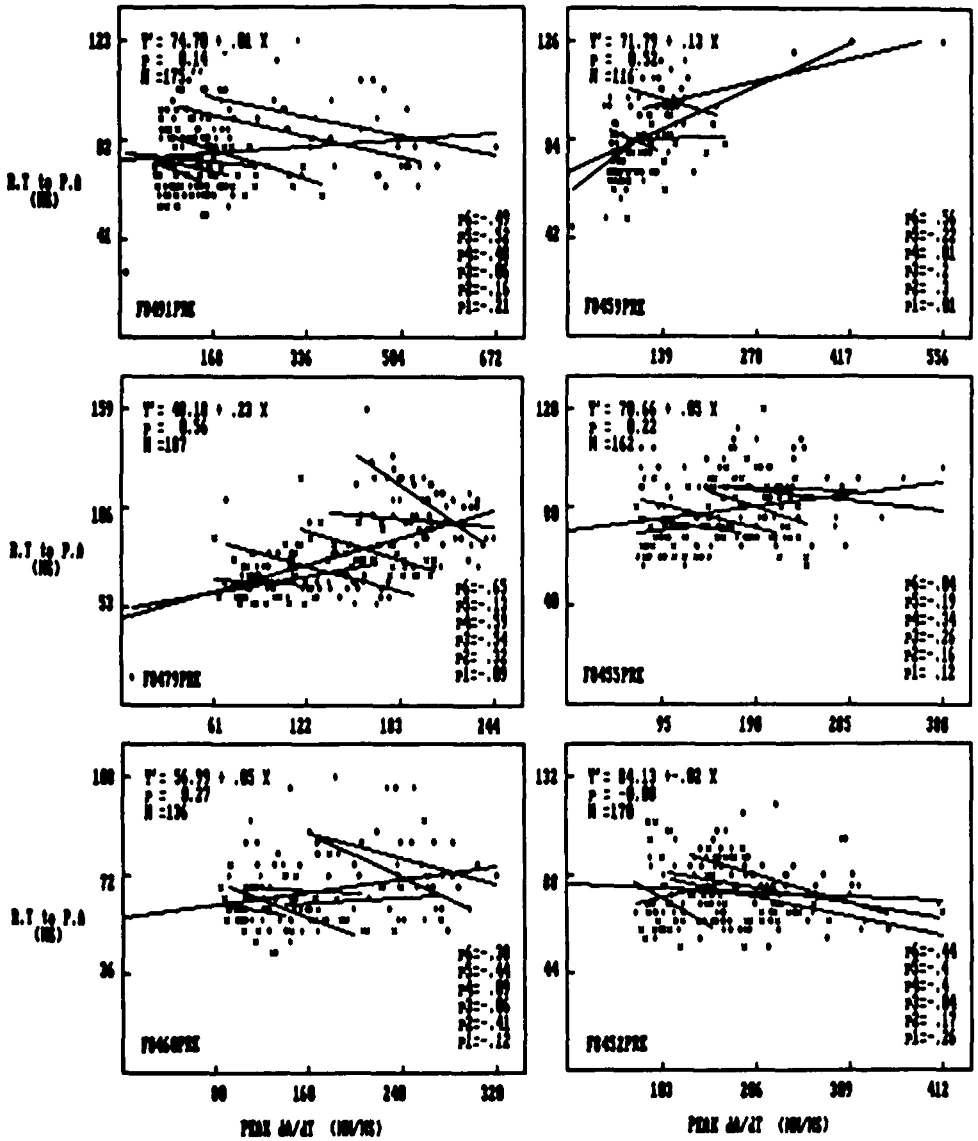


Figure 34: Correlations an regression lines (both within and across target size) between peak velocity and rise time to peak amplitude for each of the six subjects (pooling successful and unsuccessful gapes together). Legend as in Figure 30.

Table 12: Correlations, during grasping and after pooling successful and unsuccessful gapes, between peak velocity and rise time to peak amplitude, for each particular target size, for all six subjects. Sample sizes for each of the subjects ranged from 19 to 34. (*: p <.05; **: p <.01).

	Bird					
Target size	F8452	F8455	F8459	F8460	F8479	F8491
3.2	-.26	.12	-.01	-.12	-.09	-.21
3.9	.17	-.16	.30	-.41 *	.32	-.16
4.9	-.04	-.26	-.20	-.06	-.54 **	-.06
6.4	-.40 *	-.34 *	.01	.09	-.59 **	-.48 *
8.7	-.40 *	-.19	-.22	-.44 *	-.13	-.52 *
11.1	-.44 *	-.04	.56 **	-.38	-.65 **	-.49 *

It will be recalled that even when target size is held constant (Table 8) there is a significant correlation between rise time and peak amplitude. This suggests that variations in rise time account for some portion of the variance in peak amplitude not accounted for by peak velocity. On the other hand, the scaling of rise time measures to target size is not systematic and exhibits considerable individual variability (Figure 29 and Table 6). Such considerations suggest that rise time, while not the variable controlled to producing amplitude scaling, may be playing some other systematic role in the determination of peak amplitude for grasp trajectories.

This hypothesis is supported by the analysis presented in Tables 10 and 11, which indicates that target size has a much more substantial "corrective effect" under the "pulse-width" (Table 10) than under the "pulse-height" (Table 11) strategy. Indeed, in four subjects the "corrective effect" accounts for more of the variance in peak amplitude than does rise time. Finally, it should be noted that when target size and peak amplitude are held constant (Table 9) there is a negative correlation between rise time and peak velocity. Taken together, these analyses suggest that the corrective or compensatory effect of target size is made through rise time.

Figure 35 presents a model illustrating the manner in which such compensatory adjustments might operate during the execution of the response. The figure represents (as vectors) the trajectories of three jaw-opening responses made to the same target. For the top and bottom vectors the initial velocity is incorrectly scaled to target size and will result in positive (top) and negative (bottom) errors in peak amplitude. The total duration of the response is dichotomized into two phases (accelerative and decelerative) by a line indicating the point of peak opening velocity. Note that for all three trajectories rise times to peak velocity are represented as constant during the accelerative phase. If adjustments in rise time serve to compensate for errors in the initial (programmed) trajectory, such compensatory adjustments should be evident during the decelerative phase of the trajectory. Moreover, the compensatory nature of the adjustment will be reflected in a negative correlation between opening amplitude at the start of the decelerative phase (i.e., at peak velocity) and the duration of the remainder of the trajectory (i.e., "corrective rise time"). Thus for a given target size positive errors will be compensated for by a decrease in "corrective rise time", negative errors by a increase in "corrective rise time".

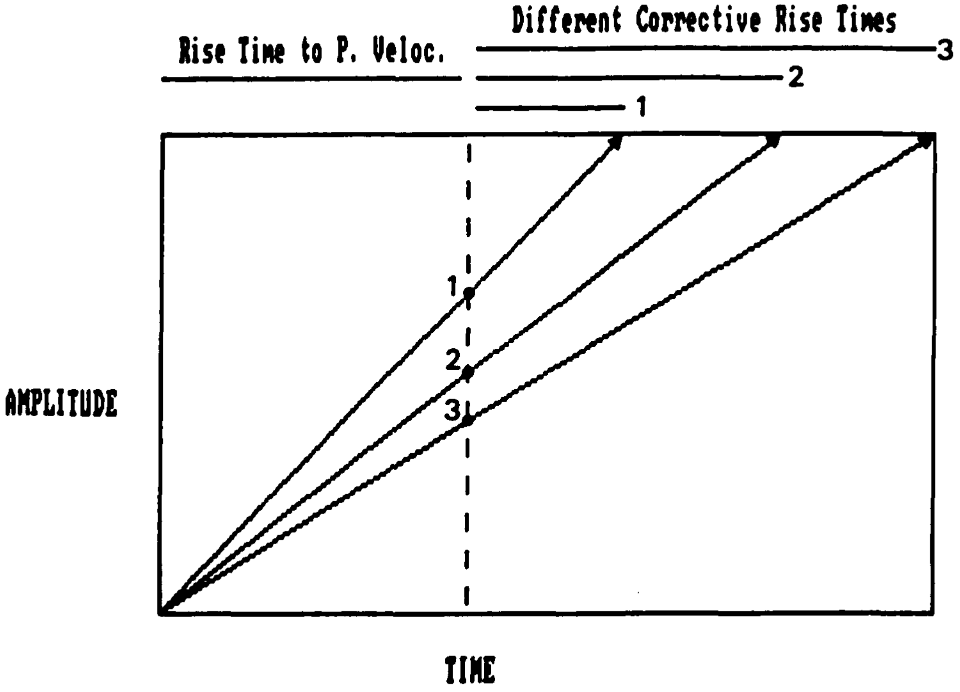


__Figure 35__: Model to explain the corrective effect of target size upon peak amplitude.

This hypothesis was tested by calculating correlation coefficients between "corrective rise time" and opening amplitudes at peak velocity within and across target sizes for each subject. Because the same trends were evident in all six subjects their data were pooled and are presented in Figure 36. Note the absence of a significant correlation across target size (r = -.07 NS). Correlations within each target size are negative and highly significant (p < .001).

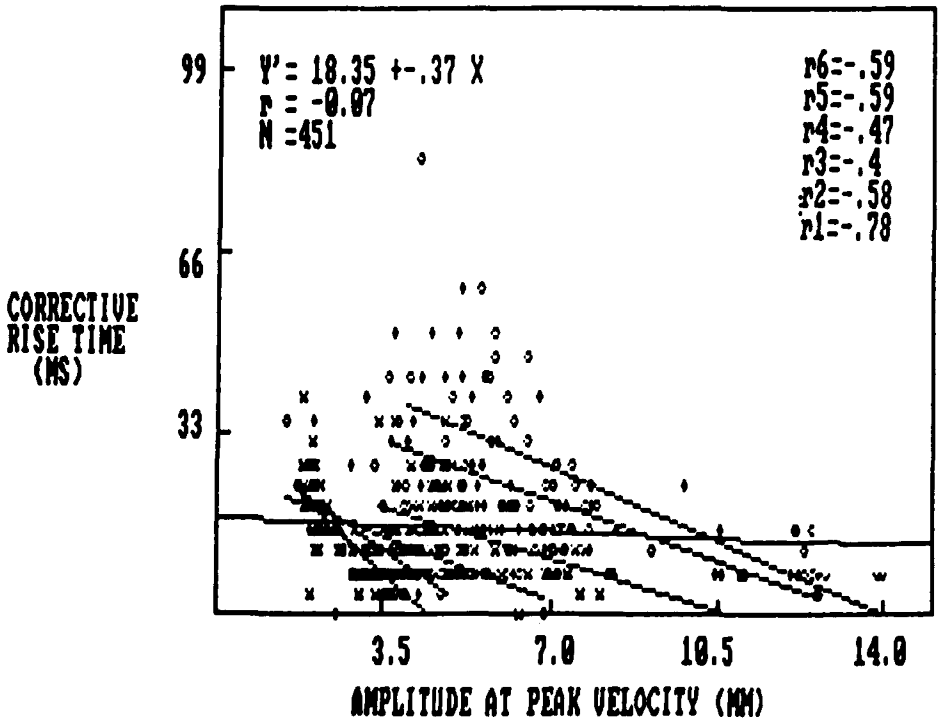


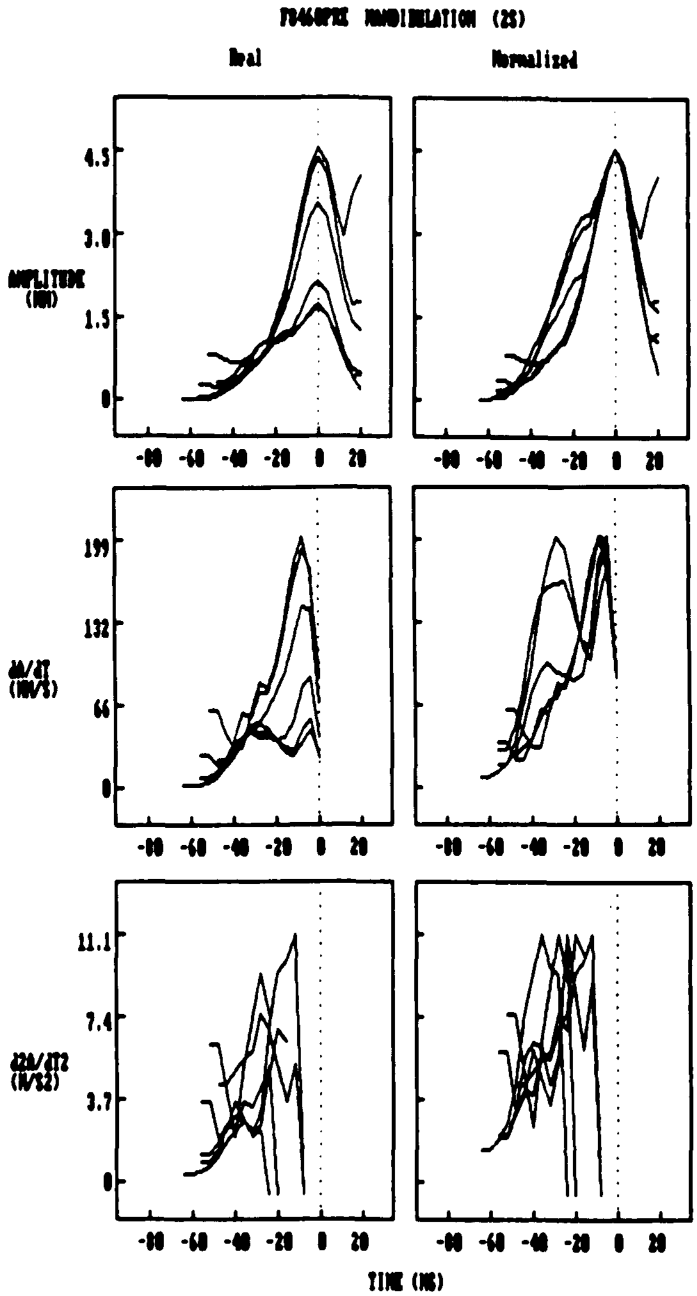
Figure 36: Correlations and regression lines between opening amplitude at peak velocity and "corrective rise time" (time from peak velocity to peak amplitude) for both within and across target sizes. Legend as in Figure 30.

Mandibulation

Relation between kinematic variables and target size.

Figure 37 presents opening trajectories associated with mandibulation for a single representative subject to illustrate the relation between movement amplitude and its first and second derivatives. Curves are aligned with respect to the peak trajectory to illustrate the relation between target size and the kinematic variable. The amplitude, peak velocity, and peak acceleration of the trajectories are scaled to pellet size. Figure 38 represents the same trajectories as before, but aligned with respect to the starting of the movement. These data suggest that rise time is inversely proportional to target size.

Functions relating kinematic variables and pellet size for a single subject are presented in Figure 39 and statistical analysis of the data for all six subjects is presented in Table 13. For the individual subject amplitude, velocity, and acceleration tend to be linear functions of pellet size, and the correlation coefficients for each of these function are significant. For the rise time measures, five of the correlations are negative, although only three of these are significant.



<u>**Figure 37**</u>: Jaw opening trajectories for amplitude, first and second derivatives across all six pellet sizes, for mandibulation. Figures on the right hand side are normalized with respect to the highest values on figures on the left hand side. Trajectories are aligned with respect to the point of peak gape.

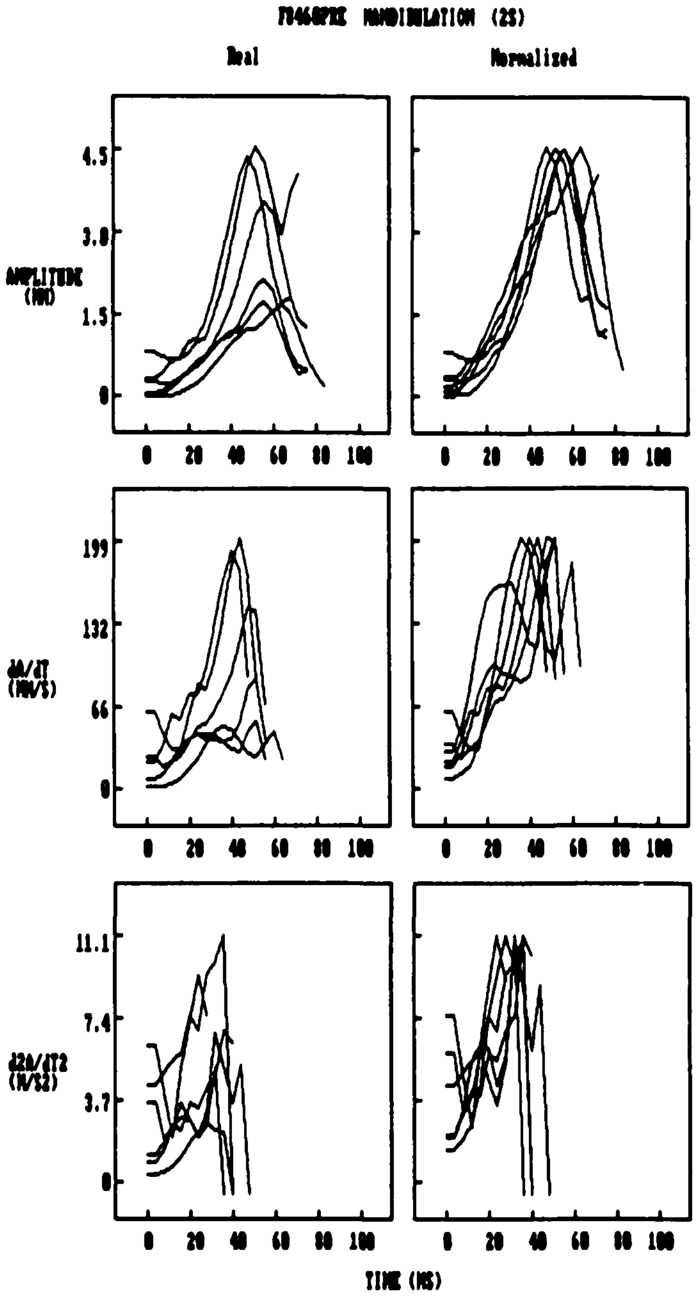


Figure 38: Jaw opening trajectories for amplitude, first and second derivatives across all pellet sizes, for mandibulation. Plots on the right hand side are normalized with respect to the highest values on plots on the left hand side. Trajectories are aligned with respect to the point of initial gape.

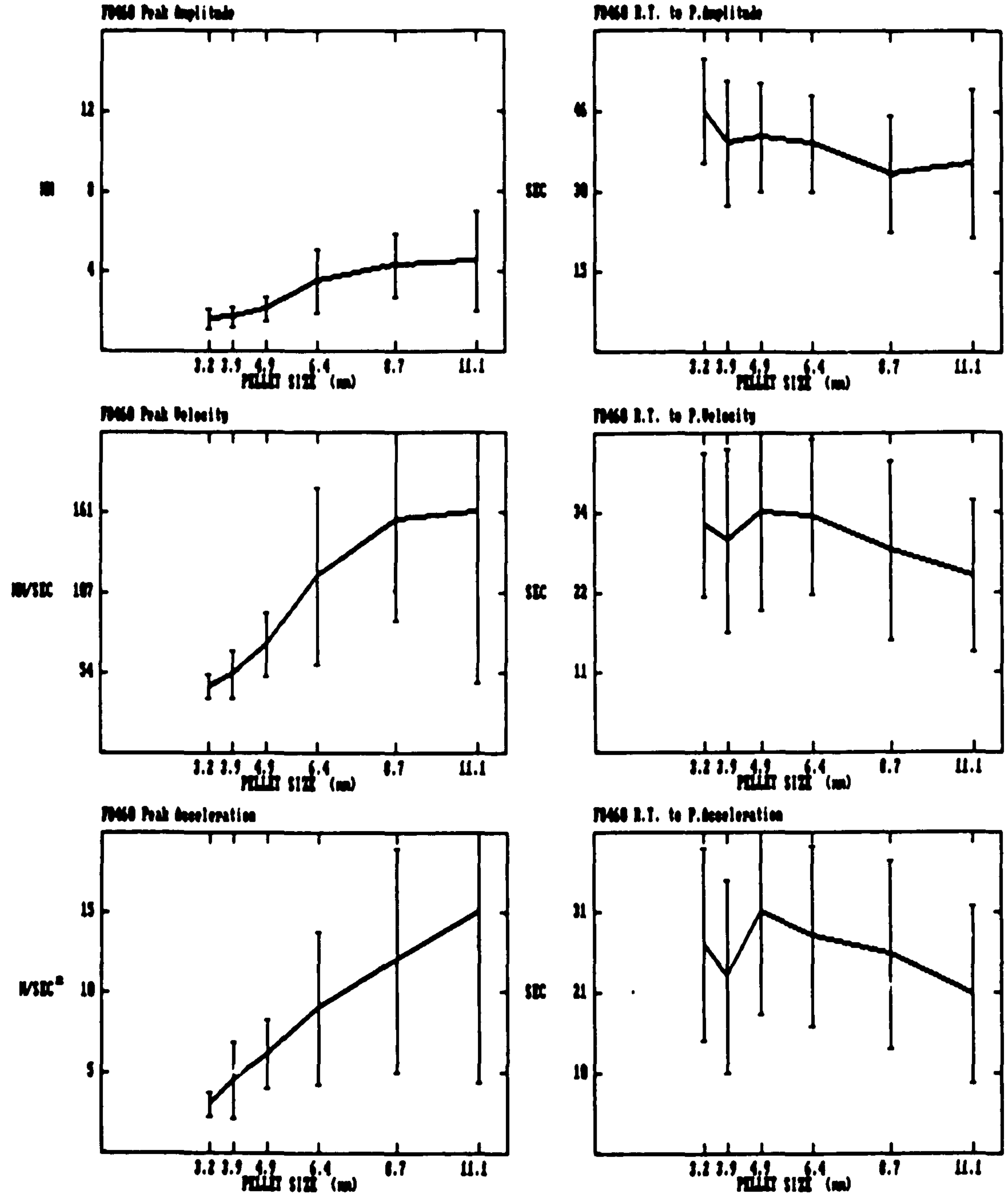


Figure 39: Functions relating amplitude, first and second derivatives with pellet size for mandibulation, as well as the functions for their respective rise times with target size. Plots are representative for a single bird (F8460).

<u>Table 13</u>: Correlations and anovas for amplitude, first and second derivative, and their respective rise times, with target size, during mandibulation. (*: p <.01; **: p <.001).

		Bird					
Variable		F8452	F8455	F8459	F8460	F8479	F8491
Amplitude	r	.77 **	.54 **	.70 **	.64 **	.58 **	.50 **
	F	23 **	7.4**	15 **	9.7**	9.5**	7.9**
Peak Velocity	r	.60 **	.56 **	.58 **	.63 **	.73 **	.64 **
	F	9.7**	7.5**	7.5**	8.9**	17 **	10 **
Peak Acceler.	r	.48 **	.54 **	.50 **	.63 **	.51 **	.64 **
	F	5.7**	7.1**	4.8**	7.9**	7.0**	9.0**
R.T. P.Amplit.	r	.21	-.34 *	-.07	-.28	-.35 *	-.51 **
	F	2.5	3.6*	.34	1.5	7.3**	6.9**
R.T. P.Veloc.	r	.10	-.48 **	-.23	-.19	-.32 *	-.61 **
	F	1.4	5.8**	.75	.82	12 **	8.9**
R.T. P.Accel.	r	-.01	-.45 **	-.36 *	-.13	-.33 *	-.58 **
	F	1.3	5.4**	2.0	.95	11 **	7.7**

Relation among kinematic variables.

To provide data bearing on the bird's motor control strategy during mandibulation, the relations among these kinematic variables were examined. Figure 40 illustrates these relations for a single subject. For each pair of kinematic variables, the regression lines between and within

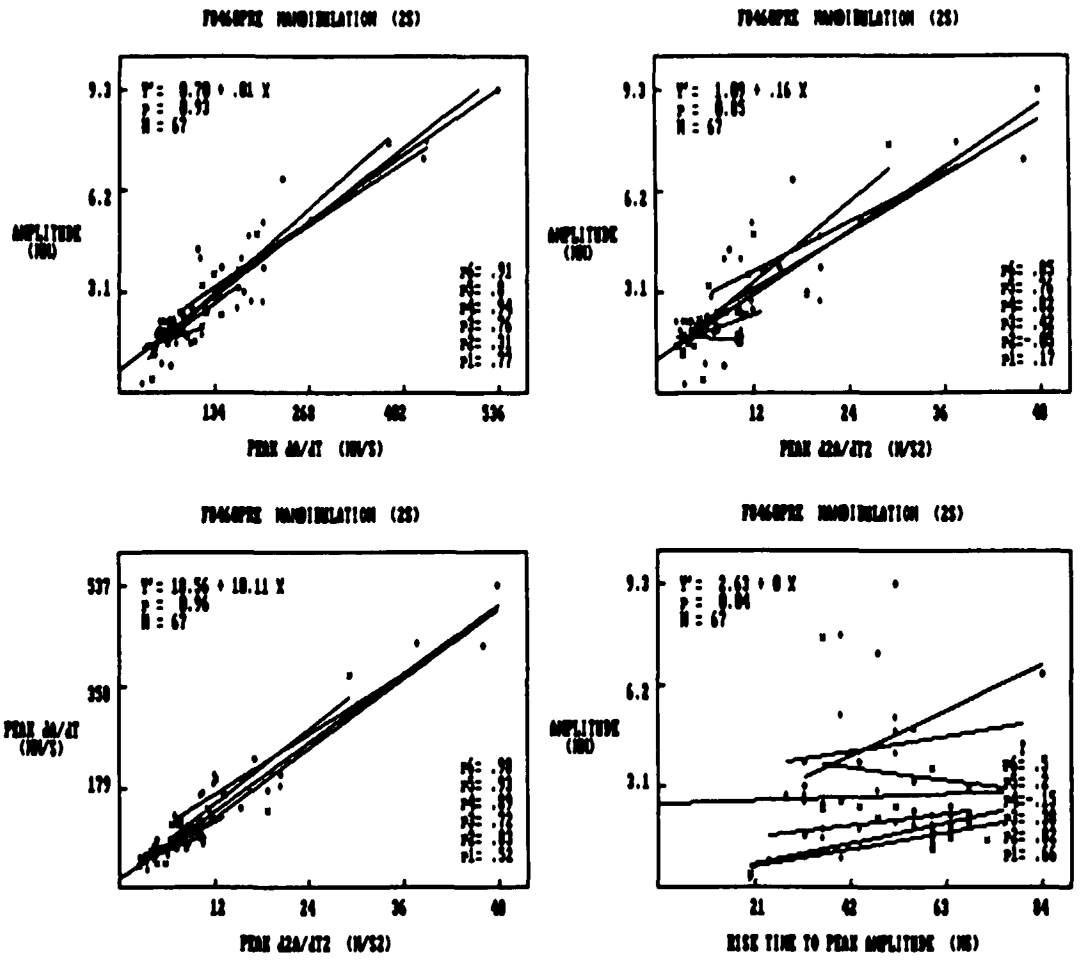


Figure 40: Regression line and correlation coefficients among kinematic variables during mandibulation. Legend as in Figure 30.

target sizes are plotted, as well as their associated correlation coefficients. As it was done for grasping, correlations were computed between the kinematic variables and peak amplitude for all six subjects (Table 14). It is possible to see that the correlations for peak velocity and peak acceleration are highly significant, while for the rise times correlations only two out of the 18 are significant.

Table 14: Correlations among kinematic variables during mandibulation. (*: p <.01; **: p <.001).

	Bird					
Variables	F8452	F8455	F8459	F8460	F8479	F8491
P.Velo-P.Ampl.	.87 **	.94 **	.79 **	.93 **	.73 **	.85 **
P.Acce-P.Ampl.	.72 **	.87 **	.55 **	.85 **	.37 **	.73 *
P.Acce-P.Velo.	.95 **	.98 **	.87 **	.96 **	.87 **	.95 **
RTPAm.-P.Ampl.	.33 *	-.02	.26	.04	.24	.12
RTPVe.-P.Ampl.	.27	-.03	.10	.11	.19	-.03 **
RTPAc.-P.Ampl.	.23	.02	-.03	.13	.19	.01

The high correlations between velocity and amplitude measures and the absence of any such correlation with rise time measures strongly suggests that mandibulation involves a pulse-height rather than a pulse-width strategy. Further support for this conclusion is provided by partial correlation and multiple regression analyses similar to those applied to grasping. The results of the first of these analyses is shown in Table 15 which compares partial correlations for each of the kinematic variables under the two models. Under the pulse-height model, peak velocity continues to account for most of the variance in peak amplitude (as in grasping), while target size makes almost no contribution. For a pulse width control policy, target size explains about 50% of the variance in contrast with 16% accounted for by rise time. Note, however, that there is a significant negative correlation between target size and rise time (when holding peak amplitude constant), indicating that as target size increases, rise time decreases.

Table 16 presents partial correlations among the four kinematic variables, taken two at a time, while holding the other two constant. A comparison of this data with that for grasping presented in Table 9 indicates that the negative relationships between peak velocity and rise time has increased and there is also a significant negative correlation between target size and rise time. That means, when the hypothetical pulse-height pathway (peak velocity and peak amplitude) is partialed out, then a negative correlation arises between target size and rise time. This could be interpreted as if within the pulse height constraints there is a tendency to decrease the rise time for the bigger target sizes.

Table 15: Partial correlations, during mandibulation, between two kinematic variables holding the third one constant. Legend as in table 8.

Variables	Bird						
Comp./Cont.	F8491	F8479	F8460	F8459	F8455	F8452	**Mean**
TS-PA/PV	-.11	.10	.19	.48**	.05	.63**	**.25**
PV-PA/TS	.80**	.55**	.88**	.66**	.91**	.80**	**.80****
TS-PV/PA	.47**	.55**	.12	.06	.18	-.22	**.20**
TS-PA/RT	.66**	.73**	.68**	.74**	.57**	.76**	**.70****
RT-PA/TS	.50**	.58**	.30*	.43**	.21	.27	**.39****
TS-RT/PA	-.66**	-.61**	-.40**	-.36**	-.39**	-.07	**-.43****

Table 16: Partial correlations, during mandibulation between two kinematic variables holding the other two constant. Second-order partial correlations were computed upon the first-order partial correlations. Legend as in Table 8.

Variables	Bird						
Comp./Cont.	F8491	F8479	F8460	F8459	F8455	F8452	**Mean**
TS-PA/PV-RT	.26	.34*	.44**	.61**	.34*	.64**	**.45****
PV-PA/TS-RT	.83**	.80**	.94**	.83**	.97**	.92**	**.90****
RT-PA/TS-PV	.61**	.81**	.74**	.74**	.78**	.77**	**.75****
TS-PV/PA-RT	.13	.11	-.24	-.25	-.20	-.40**	**-.15**
PV-RT/TS-PA	-.43**	-.71**	-.72**	-.68**	-.77**	-.76**	**-.70****
TS-RT/PA-PV	-.54**	-.35*	-.44**	-.43**	-.40**	-.35**	**-.42****

As with grasping, peak velocity does not account for all of the variance in peak amplitude. Therefore the same type of multiple regression analysis used to identify a corrective effect of target size was carried out. The analysis for a pulse height strategy is presented in Table 17 and Figure 41. As the data indicate, the addition of target size to peak velocity does not account for substantially more of the variance in peak amplitude than that accounted for by peak velocity alone. For four of the six birds there is no corrective effect, while for the other two that effect, though significant, is minimal. The percentage accounted for by peak velocity (Table 14) varied from 53% to 88% (mean across birds= 72%), and the increment introduced by the corrective effect of target size varied from 0% to 9% (mean across all birds= 3%), being significant only for two subjects (F8459 and F8452, p<.001).

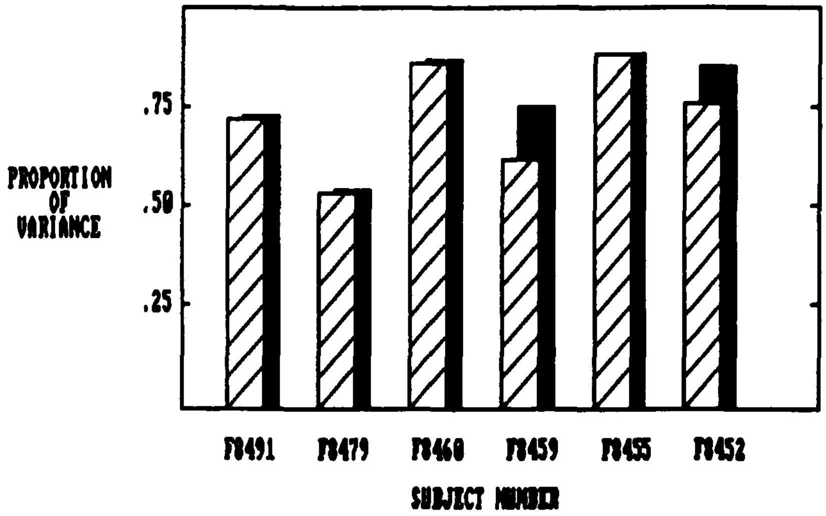


Figure 41: Proportion of variance in peak amplitude, during mandibulation, accounted for by peak velocity ($r^2_{y.1}$, dashed bars) and by the joint effect of peak velocity and target size ($R^2_{y.1,2}$, dark bars). Legend as in figure 32.

Table 17: Percentage of variance in peak amplitude, during mandibulation, accounted for by peak velocity ($r^2_{y.1}$), by the combined effect of peak velocity and target size ($R^2_{y.1,2}$), and the difference between the two of them. Legend as in Table 10.

	Bird					
Regression	F8491	F8479	F8460	F8459	F8455	F8452
$r^2_{y.1}$	73	54	87	62	88	76
$R^2_{y.1,2}$	73	54	87	71	88	85
$R^2_{y.1,2} - r^2_{y.1}$	0	0	0	9 **	0	9 **

The same analysis applied to the pathway involved under pulse width control (as shown in Figure 42 and Table 18), shows that for all the birds the variance accounted for by rise time is very small, from 1% to 10 % (mean across all subjects= 4%), while the corrective effect added from 32% to 52% (mean across all subjects= 45%), and is significant for all birds (F test, $p < .001$).

Table 18: Percentage of variance in peak amplitude, during mandibulation, accounted for by rise time to peak amplitude ($r^2_{y.1}$), by the joint action of rise time to peak amplitude and target size ($R^2_{y.1,2}$), and the difference between the two of them. Legend as in Table 10.

	Bird					
Regression	F8491	F8479	F8460	F8459	F8455	F8452
$r^2_{y.1}$	1	5	1	6	1	10
$R^2_{y.1,2}$	44	56	46	58	32	62
$R^2_{y.1,2} - r^2_{y.1}$	43 **	50 **	46 **	52 **	32 **	51 **

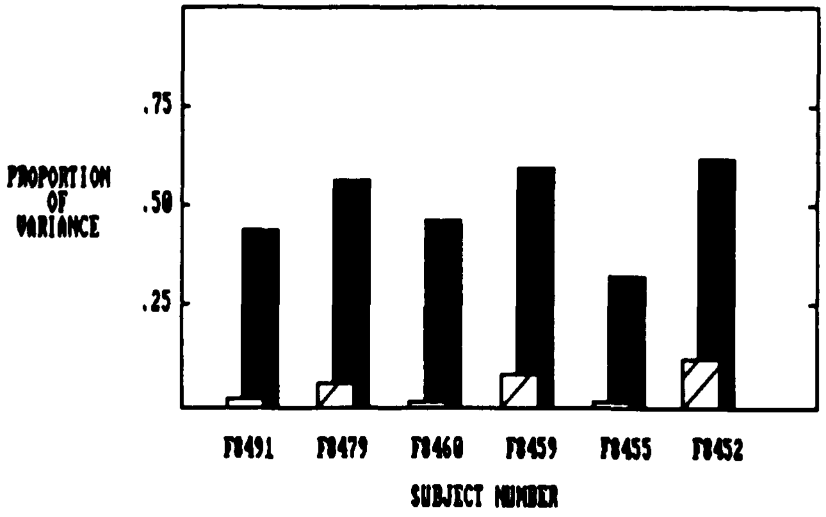


Figure 42: Proportion of variance in peak amplitude, during mandibulation, accounted for by rise time to peak amplitude ($r^2_{y.1}$, dashed bars), and by the joint effect of rise time and target size ($R^2_{y.1,2}$, dark bars). Legend as in figure 32.

Using Table 18 and the same rationale it was used before during grasping, the compensatory adjustment to the trajectory explains from 0.2% to 39% (mean = 6%) of the variance not explain by pulse height control. Again, to explain the corrective effect it is necessary to look at the correlations between peak amplitude and rise time. As it can be seen in Table 19, 23 out of the 36 correlations are negative, although only 2 are significant. These values are less significant than those for grasping, probably because this relationship is not as important as for grasping, due to the fact that the compensatory adjustment explains only 6% of the variance not explained for peak velocity, as opposed to the 46% during grasping.

Table 19: Correlations, during mandibulation, between peak velocity and rise time to peak amplitude, for each particular target size, for all six subjects. Figures were obtained after two degrees of smoothing upon raw data. Legend as in Table 12.

	Bird					
Target size	F8452	F8455	F8459	F8460	F8479	F8491
3.2	-.26	-.19	.50	.26	-.47	-.49
3.9	-.25	.33	-.24	-.05	-.50	.28
4.9	.27	-.26	.11	-.04	.30	-.06
6.4	-.10	.40	-.19	-.32	-.47	-.20
8.7	-.36	.08	-.68 *	-.37	-.23	.18
11.1	-.47	-.75 **	.44	.14	-.18	.67 *

The different ways in which birds control grasp and mandibulation (i.e. how peak velocity and rise time are controlled) are clearly reflected in Figures 43 and 44. In Figure 43 we can see the relationship between the two kinematic variables and target size, when both are normalized (upper figure for grasp movements, lower for mandibulation). This normalization permits to compare the degree of matching for both peak velocity and rise time with target size. The matching is clearly better for peak velocity, for both mandibulation and grasp. The same data are plotted in Figure 43, but this time comparing the same variable for the two movement types (upper plot for peak velocity, lower for rise time to peak amplitude).

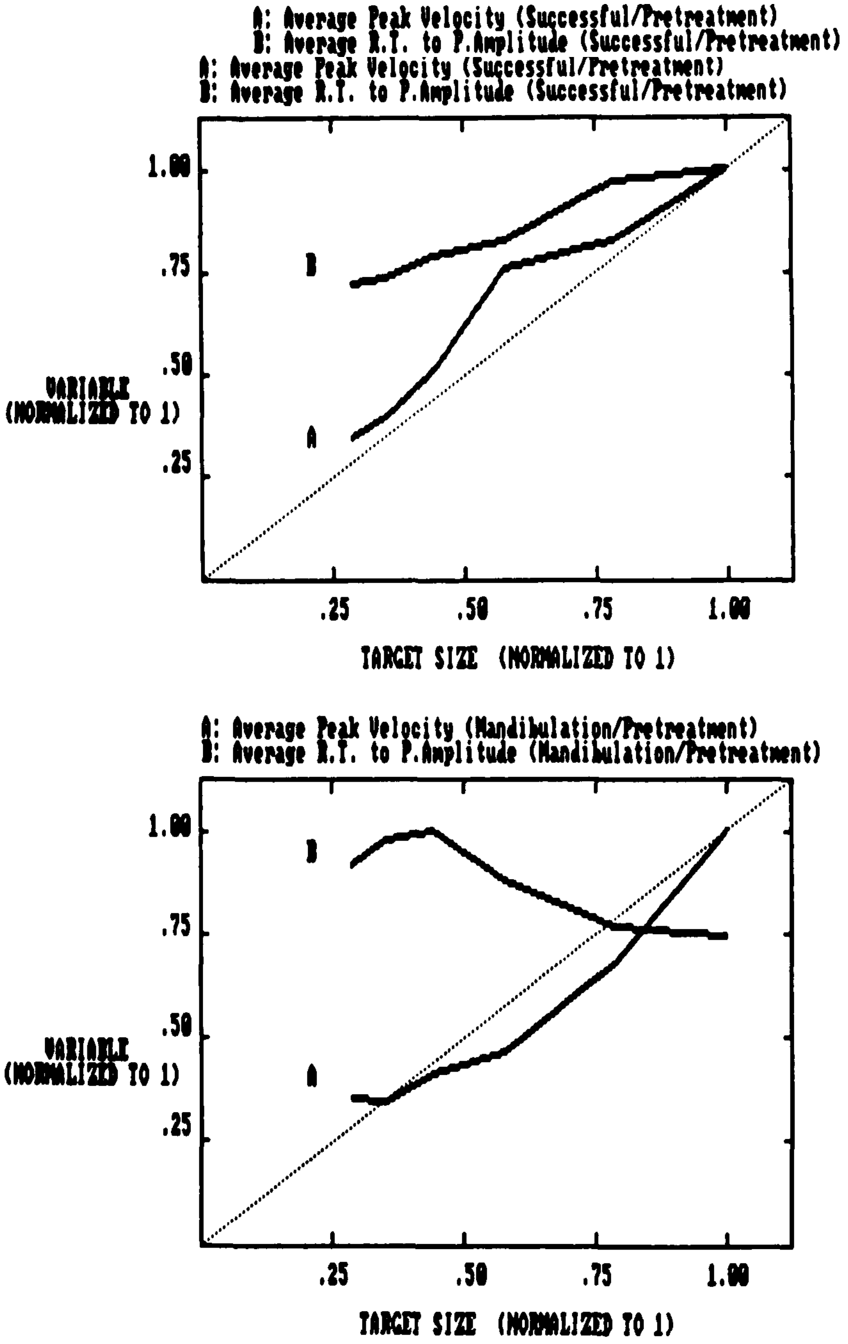
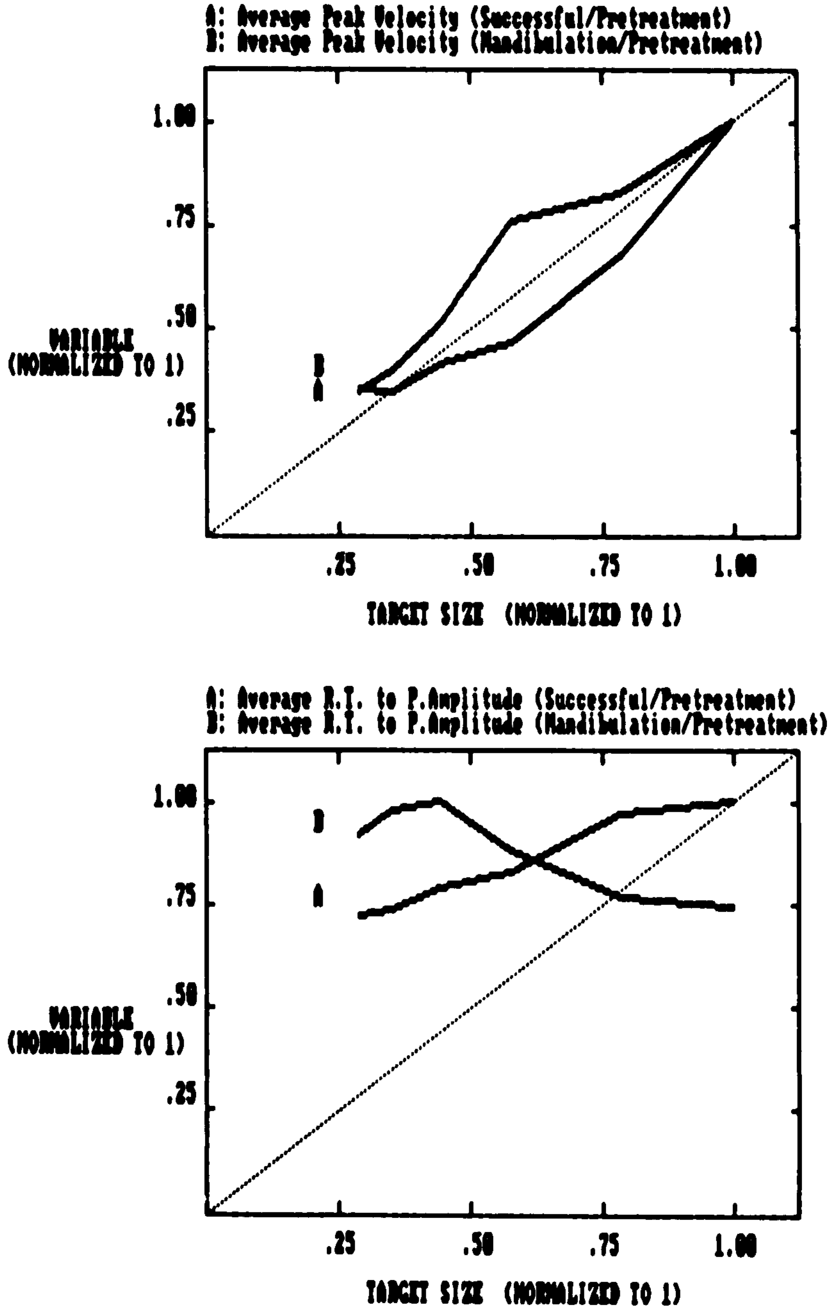


Figure 43: Peak velocity and rise time to peak amplitude functions (average of all six birds) related to pellet size. Values are normalized to 1. Upper figure represents grasp, lower figure mandibulation.



<u>Figure 44</u>: Comparison of peak velocity and rise time to peak amplitude functions, for both grasp and mandibulation, related to target size (summed across all subjects). Values are normalized to 1. Upper figure represents peak velocity, lower figure rise time to peak amplitude.

Figure 45 presents a series of schematic diagrams to illustrate the way in which opening trajectories for each of the movement classes vary with pellet size. Each line represents a vector connecting the starting and ending points of the trajectories (mean of all six subjects) within a time-amplitude coordinate axis. For grasps and mandibulation, both amplitude and time values vary with pellet size. For grasps time varies directly with target size ($r=.54$, $p<.001$) while for mandibulation this relationship is negative ($r=-.24$; $p<.001$). For prepecks and swallows the vectors are superimposed with respect to both amplitude and time and neither correlation is significant ($r=.04$; .03, respectively). Figure 46 presents the same data as Figure 45, but now just for grasps and mandibulation and for each individual subject. The overall effect it was just seen in figure 45 for grasping (of a common influence of both peak velocity and rise time), seems different, because now it is possible to realize that for every bird the amplitude seems to be accomplished by changes in the slope (pulse height), and/or by changes in the rise time (in a different contribution within each subject). The individual trajectories during mandibulation (Figure 46) seem to reflect the same principle as for the overall plot (Figure 45), that is, there is a change in slope, together with a negative relationship between target size and rise time.

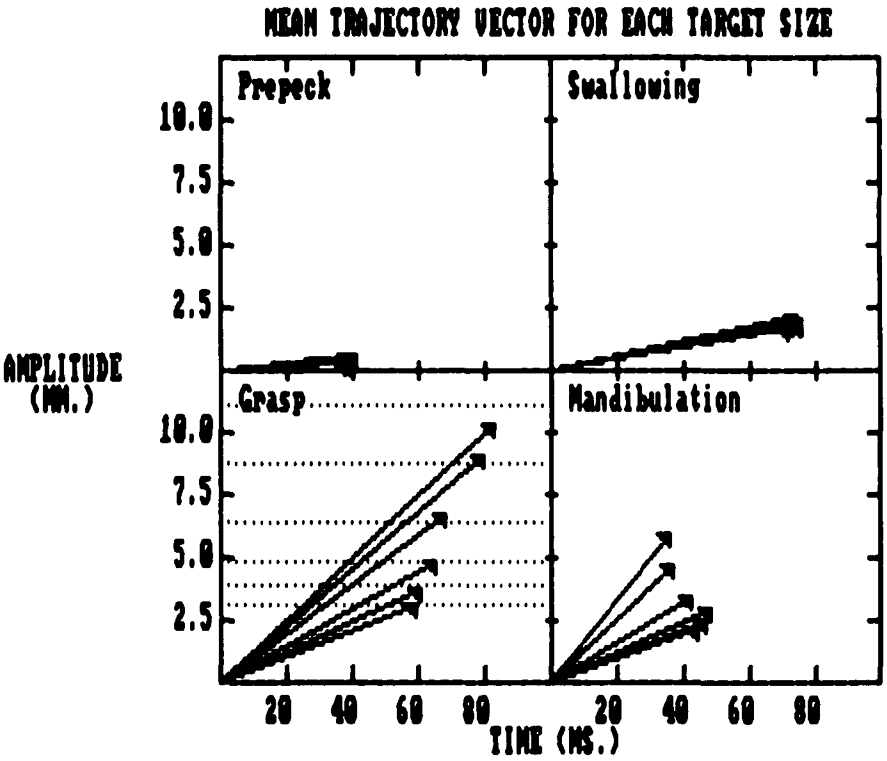


Figure 45: Mean trajectory vectors for each of the target sizes and all four gape classes. Vectors were traced by connecting the mean starting gape with the mean peak amplitude over the mean opening duration. Mean values were taken after pooling all six birds. Dotted lines on bottom left quadrant represent target values.

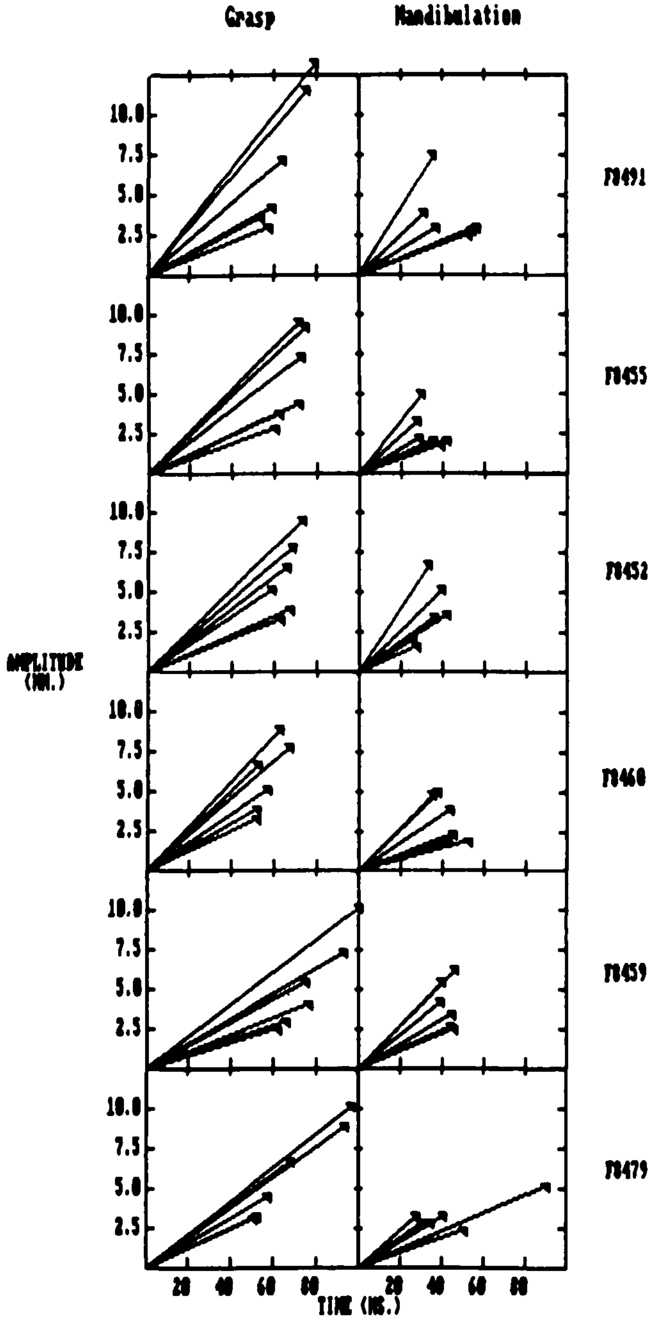


Figure 46: Mean trajectory vectors for grasps and mandibulation (for all six pellet sizes), for each one of the subjects. Legend as in figure 43.

DISCUSSION

Grasping

Kinematic analysis of jaw opening movements during grasping shows that opening amplitude and its first and second derivatives are functionally related to target size. The correlation coefficients are highly significant for all of the subjects. Furthermore, the high and consistently significant correlations between peak velocity and peak amplitude indicate that peak velocity (and peak acceleration) account for most of the variance in peak amplitude.

In contrast, evidence for function of rise time to target amplitude is neither as clear nor as consistent. While the correlation coefficients are highly significant for half the birds and the group function suggests some degree of relation, examination of the individual data reveals important differences between the functions for duration and velocity measures. By contrast with peak velocity, the rise time functions do not show consistent increments with increases in target size and reversals are not uncommon.

A comparison of the relation among kinematic variables and that between target size and these variables is also of interest. The correlations between target size and rise time are generally less significant than those between rise time and peak amplitude. These differences suggest that peak amplitude is better accounted for by target size through peak velocity than through rise time to peak amplitude, a finding which tends to support the results of the multiple regression analysis. These data indicate that the proportion of the variance in peak amplitude accounted for by peak velocity is greater than that accounted for by rise time variables. Taken together the kinematic analysis tends to support a predominant pulse-height strategy for the control of jaw opening during grasping, while a pulse-width strategy would be responsible of corrections during the same opening.

Kinematic analysis thus indicates that the motor control strategy underlying the scaling of jaw opening during grasping and mandibulation in the pigeon is similar to that used by cats and humans to control the scaling of isometric force in tasks involving limb movements (Freund and Budingen, 1978; Ghez and Vicario, 1978; Gordon and Ghez, 1985).

This similarity extends to another aspect of motor control, the capacity to adjust movement trajectories during their execution in order to correct for errors in the initial, programmed trajectory. In Woodworth's original formulation of the concept of "current control" (1899) such adjustments were presumed to be based upon peripheral feedback during the terminal portions of the response. More recently it has been shown that fast movements can be corrected by alteration during their course, either in response to the presentation of new target information (Megaw, 1974; Vicario and Ghez, 1984) or by making appropriate corrections during the execution of the movement (Gordon, 1985; Higgins and Angel, 1970).

Gordon (1985) has developed a statistical procedure involving multiple regression analysis which makes it possible to detect the presence of such corrective behavior and to calculate its contribution to the scaling of trajectory amplitude. The application of this procedure to the kinematic data for grasping provided evidence that subjects modulate rise time during the execution of the response in such as way as to correct for errors in the magnitude of the initial (programmed) opening trajectory. These findings on the role of rise time may help to account for the presence of small but significant correlations between rise time and peak opening amplitude during grasping. Such corrective adjustments, though accounting for only a small portion of the variance in peak amplitude, were evident in the data of all subjects and are a distinctive feature of the kinematics of grasping in the pigeon.

Mandibulation

As with grasping, the amplitude of jaw-opening movements during mandibulation is functionally related to target size as are their first and second derivatives. While the correlation coefficients are somewhat smaller than those for grasping, they are highly significant for all subjects and positive in direction. In contrast, only three subjects showed significant correlation between peak amplitude and rise time during mandibulation and all three of these are negative.

An analysis of the relations among kinematic variables indicates that peak velocity accounts for most of the variance in peak amplitude with essentially no contribution from rise time. In fact, the data for mandibulation provide even stronger support for a pulse-height strategy controlling jaw opening during eating in the pigeon. A comparison of the scatter plots relating the kinematic variables during grasping and mandibulation makes this point quite clearly. For grasping, even subjects with significant across-pellet correlations always showed significant rise time correlations and within pellet correlations were often small and frequently not significant. For mandibulation, rise time correlations were not significant and both across and within target size correlations for velocity and amplitude tend to be much higher.

A multiple regression analysis of the mandibulation data indicates that while this movement, like grasping, involves a pulse-height strategy, it provides no evidence for the presence of the type of corrective or compensatory process which characterizes grasping. As Tables 6 and 7 (for grasping) and 13 and 14 (for mandibulation) indicate, the effects of target size upon rise time and the effect of rise time upon peak amplitude are different for the two movement classes. During grasping, there is a significant correlation between target size and peak amplitude (holding peak velocity constant). This correlation presumably reflects the presence of the corrective effect. No such correlation is evident during mandibulation. During grasping, the correlation between target size and rise time is not significant, either with peak amplitude held constant or with both peak amplitude and peak velocity held constant. This supports the hypothesis of a corrective effect of rise time upon peak amplitude for grasping. However, as the data plotted in Figure 41 demonstrate, there is little or no increase in the variance in peak amplitude accounted for through a pathway involving target size. The absence of a corrective effect seems to be the one important difference between the kinematics of grasping and mandibulation.

In Table 20 it is also highlighted a second difference between grasping and mandibulation which does not seem obviously related to the kinematics of the two movements. For mandibulation, there is a significant negative correlation between rise time and target size which is seen with both types of partial correlations and is not present for mandibulation.

Figure 45 illustrates some general considerations which apply to the kinematics of four movements classes identified in this study. The movement trajectories are represented as vectors for each target size summed across all of the subjects. For prepecks and swallows, as it was noted earlier, there is no obvious relation between target size and either peak velocity or rise time. Such relationships do exist for grasping and mandibulation and the vectors for individual subjects are plotted in Figure 43. Three aspects of the figure are immediately apparent:

Table 20: Comparison of some mean values taken from the partial correlation tables for both grasping and mandibulation (legend as in Table 8).

	Partial Correlations		
Gape Type	TS-PA/PV	TS-RT/PA	TS-RT/PA-PV
Grasping	.68 **	-.07	-.11
Mandibulation	.25	-.43 **	-.42 **

1) For both movement types, an increase in target size seems to be paralleled by an increased slope, generally supporting the pulse-height hypothesis, but there are striking individual differences in the trajectories of the six birds.

2) In general, for a given amplitude, mandibulations have shorter rise times than grasps, although the velocity ranges of the two movement types tend to overlap.

3) Rise time tend to be shorter for the larger pellets. The functional significance of the latter observation is considered in the general discussion.

GENERAL DISCUSSION

Eating in the pigeon requires the organization of several distinct movement patterns into an adaptative behavioral sequence. While linkage among these movements patterns is provided by stimuli from the food (Zeigler et. al., 1980), each of the motor patterns itself presents an independent problem in sensorimotor integration. Considered from the viewpoint of motor control mechanisms, pecking, grasping and mandibulation are functionally equivalent to the transport, grasp and manipulation components of reaching/grasping in humans (Deich et al, 1985). However, they are mediated by a much simpler effector organ: the jaw. Several of these movements involve a rather precise adjustment of jaw position (gape) to match the stimulus characteristics of the target.

In the first part of this study we provided a descriptive analysis of the jaw-opening movements associated with each component of the eating behavior sequence. Previous studies of jaw movements during eating have used "gape" as a measure of the adjustment of jaw opening, thereby introducing a spurious overestimation of the actual movement. The focus of the analysis in the present study, therefore, was on the relation between the amplitude of the stimulus (pellet size) and the amplitude of the associated movement. Several different movement patterns were identified; prepecks, swallows, mandibulations and two kinds of grasps, successful and unsuccessful (subsequent analysis revealed that the two types of grasp were equivalent in all important aspects). The four movement classes differed considerably in the extent to which they were scaled to the target stimulus (the food pellet). For two of the movement classes, grasping and mandibulation, jaw opening amplitude was directly proportional to pellet size over the range of pellet sizes used; for prepecks and swallowing movements no clear scaling was evident.

Prepecks have not previously been identified in studies of the pigeon's pecking behavior, in part because of their extremely small amplitude (less than 2 mm) and in part because of their location during the early part of the transport component of pecking. Previous studies of pecking behavior have used cinematographic procedures which involved sampling rates which were too low to detect such movements. This analysis provided no evidence that would permit to attribute a functional significance to prepecks (e.g., some type of presetting function) but did provide evidence that they were systematically related temporally to the occurrence of certain phases of the transport component of pecking. We concluded that prepecks are likely to reflect changes in jaw position produced during the transport movement rather than movements elicited in response to the target stimulus.

A somewhat similar conclusion was reached with respect to swallowing movements. Indeed, their classification as such is based upon the fact that they occur at the end of the ingestion sequence, after the pellet has been transported to the back of the buccal cavity by mandibulation. It may be suggested that they reflect passive movements of the beak caused by activation of pharyngeal/laryngeal muscles used in swallowing, rather than direct activation of jaw muscles. However, resolution of this problem must await the utilization of electromyographic analysis of jaw movement activity during this movement component.

The remaining jaw-movements, grasping and mandibulation, differ from each other in a number of respects. Grasping is elicited by visual stimuli from the pellet; mandibulation involves somatosensory inputs from the beak tip and the oral cavity. Moreover, the functional goals of the two movements differ considerably. Grasping responses terminate with the pellet grasped between the beak tips and require an extremely accurate adjustment of opening amplitude to target size. Opening movements during mandibulation do not require such precision but must simply be larger than target size to permit passage of the pellet through the oral cavity.

In two respects, however, the responses are quite similar. Both are extremely fast movements, (30-50 ms for mandibulation; 60-80 ms for grasp) and in both the amplitude of the jaw opening movement is clearly proportional to target size. In this sense they may be considered as simple behavioral models of amplitude scaling analogous to the tasks used in many studies of human motor control.

As a first step toward the study of neural mechanisms mediating these movement patterns, a kinematic analysis of jaw-opening movements associated with grasping and mandibulation was carried out. Because of the rapidity of these movements and their amplitude scaling characteristics, the analysis was carried out within the conceptual framework provided by motor program theory in general and by the pulse-control model in particular (e.,g. Ghez, 1979; Gordon, 1985). As a first step it was determined, for each movement, the degree to which opening amplitude, its first and second derivatives and its rise time were scaled to target size over a wide range of target sizes. Next the relationships among these kinematic variables were examined in order to distinguish between pulse-height and pulse-width accounts of the kinematic processes involved. Finally, it was explored the possible role of "corrective adjustments" in the scaling of jaw-opening amplitude for each of the movements and the relation of such adjustments to specific kinematic variables.

For both grasping and mandibulation, jaw opening movements are well scaled to target size and for both, peak velocity (and acceleration) accounts for more of the variance in opening amplitude than does rise time. The data appear to support a pulse-height strategy for both movement types.

In this respect the motor control strategy underlying these movements in the pigeon is similar to that used by cats and humans to control the scaling of isometric force in tasks involving limb movements (Ghez and Vicario, 1978b; Gordon, 1985). A similar strategy was found to characterize the scaling of hand-opening amplitude during a grasping task in humans (Levine, 1982).

The similarity between the kinematics of amplitude scaling in the rapid movements of both pigeon and human extends to another aspect of motor control. In Woodworth's (1899) original formulation, the second control mechanism ("current control") envisaged the possibility of adjustments to the trajectory during its terminal portions. These adjustments were presumed to be based upon peripheral feedback (e.g., visual or proprioceptive inputs). More recently, however, it has been shown that fast movements can be corrected by alteration during their course, either in response to the presentation of new target information (Megaw, 1974; Vicario and Ghez, 1984), or by making appropriate corrections during the execution of the movement (Higgins and Angel, 1970; Vicario and Ghez, 1984).

Applying Gordon's analysis to the kinematic data of the present study indicates that such corrections are present for opening movements during grasping. These adjustments are mediated by the modulation of rise time in such a way that overshoots in the initial amplitude trajectory are compensated for by reduced rise times while undershoots are corrected by increasing rise time. In this respect, too, these findings for grasping in the pigeon are similar to those reported by Gordon for a task involving the rapid scaling of isometric force. As in the human subjects, most pigeons achieved considerable accuracy in their scaling by controlling initial velocity, but the corrective effects of rise time, while small, are seen in varying degrees in all subjects.

These findings on the role of rise time may help to account for the fact that relatively small but significant correlations of rise time and peak opening amplitude are characteristic of opening trajectories during grasping. No such corrective adjustments are seen during mandibulation, an observation consistent with the absence of significant correlations between rise time and peak amplitude for those movements.

This difference between the two types of jaw movement may reflect differences in the functional requirements of the two types of tasks, the inputs available and the speeds at which they are carried out. As it was noted earlier, the control of opening amplitude during grasping is extremely precise, with every increment in stimulus magnitude eliciting an almost exactly proportional change in response output. In contrast, the amplitudes of mandibulations are neither constant nor exactly proportional to pellet size. Moreover, rise times for grasping (60-80 ms) are considerably longer than those for mandibulation (30-50 ms). Indeed, for movements of the same amplitude rise times for mandibulation may be half as long as those for grasping. Furthermore, every grasping movement tends to start from the same initial gape, while the starting gape for mandibulations will vary both with the size of the pellet and its location within the oral cavity. The initial somatosensory feedback about jaw position will be relatively constant for grasping and highly variable for mandibulations. The speed at which opening movements during mandibulation are carried out may be incompatible with corrective adjustments of the type seen in grasping.

Moreover, when the nature of the task the bird faces during mandibulation is considered, a tradeoff between accuracy and speed may be appropriate. It should be recalled that during mandibulation the head is being rapidly raised and the pellet transported to the back of the oral cavity by a series of "catch and throw" movements (Zeigler, et al., 1980; Zweers, 1982). Between "catches" the pellet is suspended within the oral cavity while the beaks are some distance apart. Thus the pigeon's task is to generate jaw opening movements sufficient in amplitude to allow for passage of the pellet within the oral cavity, but rapid enough to prevent the pellet from falling out of the mouth during each of these "throw" movements. In view of these considerations, it is interesting that the rise time of opening movements during mandibulation is negatively correlated with pellet size.

Conclusions: implications for future research

Despite the differences in species and methodology between the present study and previous work with humans, there is a surprising degree of similarity in their results. This finding suggests that the framework provided by pulse-control theory has considerable generality for the kinematic analysis of movement. Moreover, the present study will provide normative data for experimental studies which may help to clarify some of the neural mechanisms mediating the control of grasping and mandibulation in the pigeon.

One approach to an analysis of such mechanisms involves considerations of the role of peripheral sensory inputs in mediating the pulse-height strategy revealed by these experiments. Such inputs could be used to monitor the extent of initial gape or the degree of jaw opening. A major source of such inputs could be trigeminal afferents arising in the oral region and mediated by mechanoreceptors sensitive to tactile inputs from the pellet or proprioceptive inputs from joint receptors. The jaw opening muscles of the pigeon have few if any muscle spindles (Wild and Zeigler, 1979) but inputs from closer spindles could be used to monitor opening (Dubbeldam, 1984). Studies examining the effects of trigeminal deafferentation upon the accuracy of amplitude scaling and its kinematics are currently in progress in Zeigler's laboratory.

A parallel approach is suggested by the fact that circuits linking trigeminal sensory input to jaw motoneurons have been defined for both telencephalic and cerebellar structures (Wild, Arends and Zeigler, 1985; Arends and Zeigler, In prep.). A combination of lesions of specific nuclear regions or pathways and kinematic analysis could clarify the contribution of some of these regions to the control of jaw movement.

However, the most appropriate starting point for future studies would be an examination of electromyographic data from the jaw musculature during each of the movement patterns. It should be kept in mind that the movement trajectories which formed the subject matter of our kinematic analysis represent the coactivation of two distinct jaw muscles; the protractor of the maxilla and the depressor of the mandible. The work of Klein et al (1985) has demonstrated that both muscles are involved in generating the gapes used in grasping. Electromyographic study of their activation patterns could clarify the neuromotor mechanisms mediating the kinematics of grasping. Similarly, an EMG analysis should clarify the differential contributions of the two opener muscles to grasping and mandibulation.

The precision of the amplitude scaling shown during grasping, the simplicity of the effector system involved and the ease with which the behavior may be elicited and brought under experimental control suggest that the pigeon could provide an excellent preparation for single-unit studies of motoneuron recruitment mechanisms. Finally, the pigeon's ingestive behavior involves the generation by the same effector system, of several functionally and topographically distinct movement patterns (grasping, mandibulation and drinking). Thus in addition to its relevance for the problem of amplitude scaling, the pigeon may provide a useful model system for the study of "motor program switching" (Croll, Davis and Kovac, 1985).

APPENDIX A

Data smoothing procedure

The spatiotemporal organization of jaw movement trajectories, like those of many other simple joint movements, approximates a sigmoidal function characterized by three different phases. The movement begins with an **accelerative** phase, in which the absolute spatial increase over the same unit of time is very small but exhibits the greatest relative increase. In the second (**velocity**) phase, the increments in amplitude over units of time are larger. The third (**decelerative**) phase, exhibits smaller relative increases per unit time and ends with the peak of the trajectory. Although the shape of jaw opening movement trajectories in the pigeon resemble quite well this sigmoidal function, it has to be kept in mind that the descriptions of spatiotemporal organization of movements are digital transformations of analogue events. Thus, no matter how good the resolution of the measurement system, the space between two consecutive points must be filled in with a straight line. If the fact is added that spurious contaminating factors could also introduce some kind of noise in the A/D read-out (both spatial and temporal), then it could end up with a zigzag-like curve, although roughly approximating a sigmoidal. As an example, I could say that in the system I have been using, an error of ± 1/100 mm in the measurement of gape at a specific point, would carry on an error of ± 2.5 mm/ms in the first derivative (dA/dt), and if that error should occur in two consecutive points then the error at the second derivative (d^2A/dt^2) would be $\pm$ 0.625 m/ms^2. I have computed the percentage of error expected on peak values for gape, amplitude, first derivative, and second derivative for all the six pellet sizes. When the raw data values are artificially increased by the amount of one A/D count (standard measurement error inherent to the system), an error is obtained for gape that varied from 1.6% for the small pellets up to 4.4% for the big ones, while that error was magnified considerably at the first and second derivatives (see Table 21).

For these reasons it is customary to smooth the data in order to reduce variability associated with differentiation into first and second derivatives. While smoothing reduces the absolute magnitudes of trajectories values, it maintains intact their overall shape, providing information on their spatiotemporal organization. As a result, what smoothing does is to approximate the trajectory to a differential equation, one in which an unknown function exists along with its derivatives of various orders, an equation for finding the unknown function.

We examined the effects of several degrees of smoothing upon the variables under study. Data points for each degree of smoothing were obtained by applying a three-points running average over the previous data points. As we can see in Figure 47, the effect of smoothing is minimal for peak amplitude, while for peak velocity and peak acceleration it produces considerably lower values, due to the fact that those two variables are derived from peak amplitude. In contrast, the effect upon rise time variables is a substantial increase in their values. The main effect of smoothing upon the correlations between the different variables (Figure 48), was that the second derivative (i.e. acceleration), whose correlation with peak amplitude, while significantly positive with raw data, it became much more clear after just two consecutive degrees of smoothing.

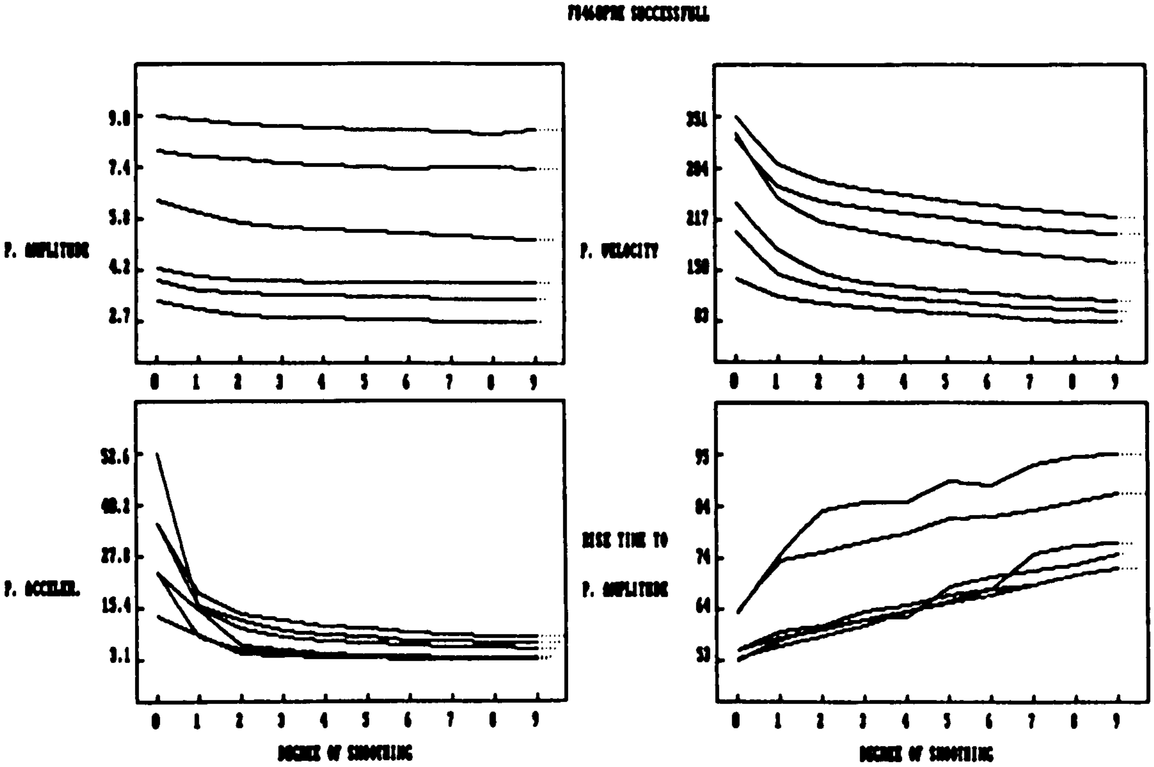


Figure 47: Effect of different degrees of smoothing upon the values for 4 of the variables. Number of dots after each line (from one to six) represent the different pellet sizes (one dot for the smallest, 6 dots for the biggest). Data points for a particular degree of smoothing were obtained by applying a three-points running average over the previous data points

In general, the maximum effect takes place with two degrees of smoothing: the quantitative aspects of some variables get smaller, while the qualitative ones get emphasized, along with some others that do not apparently change (rise times).

Data points obtained under this criteria (two degrees of smoothing) were compared against those obtain by a single 5-points running average. Such a comparison showed that the former smoothing type procedure more closely approximates.

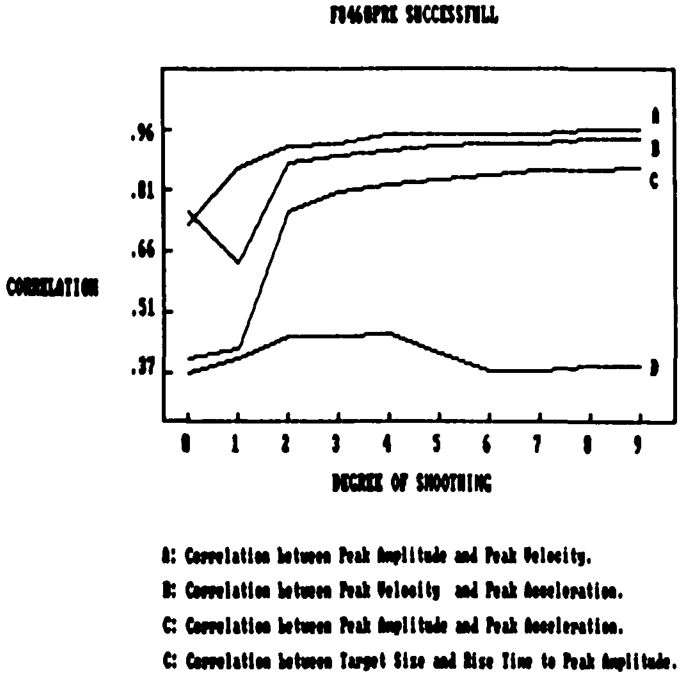


Figure 48: Effect of different degrees of smoothing upon some of the correlations among different variables. Data points for a particular degree of smoothing were obtained by applying a three-points running average over the previous data points.

Table 21: Percentage of error in gape, amplitude, peak velocity, and peck acceleration, introduced by adding one A/D count upon each raw data point. The figures are mean values obtained from all the successful pecks from a preoperative bird (F8460).

Pellet		Gape	Amplitude	Velocity	Acceleration
3.2	raw data	4.00	3.35	139.64	13.95
	+1 count	4.07	3.44	160.05	23.04
	error	1.75%	2.68%	14.61%	65.16%
3.9	raw data	4.76	4.02	202.60	24.06
	+1 count	4.84	4.12	239.47	41.89
	error	**1.68%**	2.48%	18.19%	**74.10%**
4.9	raw data	5.11	4.40	238.96	23.92
	+1 count	5.2	4.5	279.09	41.24
	error	1.76%	2.27%	16.79%	72.40%
6.4	raw data	7.50	6.46	332.05	52.63
	+1 count	7.70	6.69	396.39	77.77
	error	2.66%	3.56%	19.37%	47.76%
8.7	raw data	9.28	7.97	323.14	35.93
	+1 count	9.52	8.23	413.24	53.59
	error	2.58%	3.26%	27.88%	49.15%
11.1	raw data	10.45	9.00	351.32	35.84
	+1 count	10.92	9.49	419.99	51.22
	error	4.49%	5.44%	19.54%	42.91%

* Numbers in boldface are the extreme errors.

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