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City University of New York PH.D. 1983

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SEED GRASPING IN THE PIGEON (<u>COLUMBA</u> <u>LIVIA</u>): BEHAVIORAL ORGANIZATION AND FINAL COMMON PATH

by

Bradley G. Klein

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.

1983

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

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Abstract

SEED GRASPING IN THE PIGEON (COLUMBA LIVIA): BEHAVIORAL ORGANIZATION AND FINAL COMMON PATH

by

Bradley G. Klein

Adviser: Professor H. Philip Zeigler

This study reflected the application of a peripheral to central strategy in attempting to understand the neural control of vertebrate ingestive behavior. High speed cinematography was combined with peripheral nerve sections to study normal topography, spatiotemporal organization and peripheral motor control of the opening-grasping component of the pigeon's eating response. This component was chosen since: 1) it differentiates eating from drinking, 2) it is easily quantifiable, 3) it is under the stimulus control of an easily quantifiable stimulus variable and 4) it is presumably under the control of only two muscles. Experiment 1 examined the control of individual jaw movements during opening-grasping, as well as the basis for adjustments of gape to seed size. Experiment 2 examined the final common path for opening-grasping. Changes in both the velocity and duration of mouth opening were found to be responsible for adjustments of gape to seed size. An analysis of the factors mediating the changes in duration of mouth opening revealed that efferent systems controlling the jaws and the neck must be involved in gape adjustments. Closer examination of jaw movements during opening-grasping revealed that both jaws open for all seed sizes (from 4.1 mm to 9.1 mm), with the amount of displacement of each jaw varying with seed size. Furthermore, opening of the upper jaw preceded that of the lower jaw. Given the morphological arrangement of the pigeon skull (coupled kinesis) this suggested that the protractor quadrati muscle was involved in beak opening as well as the depressor mandibulae muscle. Sections of the motor nerves to the jaw opener muscles supported the view that M. protractor quadrati is involved in opening-grasping and established that the depressor mandibulae nerve and the protractor quadrati nerve compose the final common path for this behavior. Seed grasping appears functionally, behaviorally and neurally analogous to visually guided grasping in other vertebrates. Further examination of the neural control of seed grasping therefore promises to be of great interest in attempting to uncover common mechanisms of visually guided behavior, as well as common mehanisms of ingestive behavior in vertebrates.

Acknowledgements

I would like to thank my advisor, Dr. H. Philip Zeigler, for the intellectual, emotional and financial support which he has provided during the course of this work. I am especially grateful for the great deal of time and effort which he devoted to this project in the final stages of its preparation. I also thank him for his friendship over the past several years.

I would also like to thank the members of my supervisory committee, Dr. James Gordon and Dr. Peter Moller, for their thoughtful advice. I also thank my outside readers, Dr. Walter Bock and Dr. Joshua Wallman for their comments and critisisms.

Special thanks are in order for Dr. James Deich who unselfishly helped me with many aspects of the data analysis. I would also like to thank him for writing the software which enabled me to use the Apple Graphics Tablet for analysis of the feeding films. He has not only been a colleague, but a surrogate mentor in Dr. Zeigler's absence. I will always be grateful for the friendship and generosity which he and his wife Alice have shown towards me.

Heartfelt thanks are also in order for Mrs. Agnes Reilly, who provided technical assistance in almost every facet of this project. Moreover, I would like to thank her for her friendship, her advice and for the genuine concern which she has shown for me. I will always consider her a memeber of my family.

I would like to thank Dr. Martin Wild for teaching me the surgical skills necessary for this dissertation. I also thank Dr. Herman Berkhoudt for instruction in electrophysiology and the horseradish peroxidase technique.

I also thank the many friends, both students and faculty, with whom I have shared the "Biopsychology experience". Your companionship is one of the positive memories which I will always associate with graduate school. I would also like to thank Dr. Mark Jacquin for introducing me to my new friends and colleagues at Rutgers University, and Dr. Robert W. Rhoades for helping me prepare the grant which secured my post-doctoral fellowship.

I above all thank my wonderful wife Rita, for providing both understanding and strength during many stressful periods. I especially thank her for her help in preparing this manuscript. I hope that I can be as helpful to her during the preparation of her dissertation.

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General Introduction

Over the past several years, neurobehavioral investigations of ingestive behavior have focused on the role of central neural structures in controlling the intake of food and water. This central approach resulted from early lesion and stimulation studies of the hypothalamus. Hetherington and Ranson (1940) showed that destruction of the ventromedial hypothalamus (VMH) in rats resulted in voracious overeating to the point of obesity. On the other hand, stimulation of the VMH was found to inhibit eating in hungry rats (Margules and Olds, 1962; Hoebel and Teitelbaum, 1962). Observations such as these led to the VMH being labelled a "satiety center". Lesions of the lateral hypothalamus (LH) in rats and cats resulted in a syndrome which severely disrupted food and water intake (Anand and Broebeck, 1951; Teitelbaum and Epstein, 1962), while stimulation of the LH could elicit eating and drinking behavior (Miller, 1963; Mogenson and Stevenson, 1967). The LH was subsequently labelled a "hunger" or "initiation center", which complemented the "satiety center" (Thompson, 1975).

This "hypothalamocentric" view of the control of ingestive behavior is limited in terms of both behavioral and neuronal specificity. For example, non-ingestion specific behavioral deficits have been observed in LH lesioned rats. Marshall, Turner and Teitelbaum (1971) have observed problems with head orientation responses to olfactory and somatosensory stimuli in these animals. Furthermore, Stricker and Zigmond (1975) noted that LH lesioned rats show impairments in any voluntary activity that requires sustained alertness.

The anatomical complexity of the hypothalamic region may account for the diversity of behavioral effects which result from lesions of the VMH and LH. According to Grossman (1979), the lateral hypothalamus is traversed by numerous diffuse fiber systems and has no clearly demarcated cellular groups. Although specific nuclei can be discerned in the VMH, the area is also a region of passage for many fiber tracts. Therefore, lesions of the LH and VMH are likely to produce varying degrees of damage to sensory, motor and neurochemical pathways coursing through the diencephalon (Zeigler, 1983). Given the heterogeneous nature of this area of the forebrain, and the diversity of deficits produced by its destruction, the utility of the "hypothalamocentric" approach for relating specific neural subsystems to specific ingestive functions appears questionable.

An alternative approach to the study of ingestive behavior is to begin peripherally, with the overt behavior, describing its topography and spatiotemporal organization, and identifying its afferent and efferent mechanisms (see Dethier, 1976; Zeigler, 1976). The analysis then proceeds centrally, identifying the interneurons involved at subsequent levels of the nervous system. Such an approach involves the systematic application of behavioral, anatomical and physiological methods to the preparation of interest. It has been widely used in the study of invertebrate behaviors such as the gill withdrawal reflex of Aplysia (see Kandel, 1976) and the escape response of the crayfish (Zucker, Kennedy & Selverston, 1971), and is gaining wider acceptance among students of vertebrate behavior (see Cohen, 1969; Kow & Pfaff, 1977). This approach facilitates the identification of the behavioral function of discrete neural elements.

A reluctance in adopting such a strategy for the study of ingestive behavior has resulted from a conceptual dichotomy between motivational and sensorimotor mechanisms (Zeigler, 1983). Inherent in this dichotomy is the view that "higher level" motivational mechanisms are controlled by central structures while "lower level" sensorimotor mechanisms are controlled by peripheral structures. The validity of this view is questionable in light of recent work on the trigeminal system of birds and mammals. Lesions of central trigeminal structures in the pigeon (including the principal sensory nucleus, the quinto-frontal tract and nucleus basalis) produce deficits in both the sensorimotor control of eating and in responsiveness to food (Zeigler, 1976). Similar results have been demonstrated following peripheral trigeminal deafferentation in the pigeon (Zeigler, 1976). Peripheral orosensory deafferentation in the rat has also been found to disrupt both responsiveness to food and water, as well as the sensorimotor control of eating and drinking (Jacquin and Zeigler, 1983). It should also be noted that more recent analyses of ingestive behavior in LH lesioned rats have identified deficits in the sensorimotor control of ingestion (Turner, 1973).

The relationship between central and peripheral structures in the control of ingestive processes supports the feasability of a systematic peripheral to central strategy for examining ingestive behavior. This dissertation reflects the application of such an approach to a "model system" for vertebrate ingestive behavior: the eating response of the pigeon (Columba livia).

According to Cohen (1975), a "model system" should meet the following criteria: 1) the behavior should be amenable to spatiotemporal description and the quantification of its response dynamics. 2) It should reflect the neural processes for which it is meant to serve as a paradigm. 3) The results obtained with the "model system" should be broadly generalizable to traditional mammalian laboratory preparations and 4) the "model system" should allow the experimental study of a broad range of questions.

The eating response of the pigeon appears to amply satisfy all these requirements. 1) It is a species-typical, stereotyped movement pattern whose spatiotemporal organization can be characterized along a time scale similar to that used by the neurophysiologist (milliseconds) (Zeigler, Levitt and Levine, 1980). 2) The rate and temporal distribution of eating are sensitive to a variety of motivational variables (Zeigler, 1976). 3) A growing body of evidence supports the validity of generalization from avian to mammalian nervous systems. For example, there are marked similarities in central projections and response properties of avian and mammalian trigeminal systems (see Smith, 1973; Zeigler & Witovsky, 1968). 4) The response is relevant to several other areas of investigation such as motivation, motor control and plasticity.

Motion picture analyses of eating in the pigeon by Zeigler, Levitt and Levine (1980) and Zweers (1982) have revealed that the response is comprised of an integrated series of distinct movement patterns: fixation, pecking, grasping, stationing, transport and swallowing. The response begins with fixation, during which the animal positions its head, with beaks closed, above the seed to be consumed. During pecking, the head descends toward the seed as the eyelids begin to close. Grasping is integrated into the pecking component and may be subdivided into an opening and a closing phase. Beak opening begins about 25-30 milliseconds (msec) prior to contact with the substrate. Beak closing is initiated at substrate contact and terminates with the seed held firmly within the beak. In stationing, the eyelids open, and through a rapid deceleration of head withdrawal, the seed is thrown to a more caudal position within the beak. During transport, the tongue carries the seed back to the esophagus where swallowing takes place.

The topography of eating suggests that it involves the coordination of a series of response systems, each of which presents an independent problem in sensorimotor integration. For example, fixation might be one system, involving a coordinated output of head and neck musculature based on information regarding seed position. Transport might be another system, involving a coordinated output of tongue musculature based on tactual input from the seed. A neurobehavioral analysis of eating should therefore proceed in three stages: 1) determine the topography and spatiotemporal organization of the response, 2) determine the neural control of each response system and 3) determine the neural mechanism which coordinates these systems to produce normal eating topography.

For several reasons, the opening-grasping component of eating appears to be a desirable starting point for such analyses. First, this component appears to be the major topographic feature which differentiates drinking and eating. In drinking, the beak remains almost closed during head descent (Klein, LaMon & Zeigler, 1983). Therefore, the presence of opening-grasping can be used as a behavioral indicator of activity in the neural system mediating hunger. Second, opening-grasping is easily quantifiable. Photographic analysis reveals that the amount of mouth opening (gape) prior to seed contact varies in a linear fashion with seed diameter over a range of seed sizes from 1.5 to 10.5 mm. Therefore, opening-grasping appears to be under the stimulus control of an easily quantifiable stimulus variable. Another important reason for beginning a neurobehavioral analysis of eating with opening-grasping is that mouth opening appears to involve the operation of only two muscles, the openers of the upper and lower jaws. This promises a much simpler analysis of the final common path mechanisms than other components of the eating response such as pecking or transport, which probably involve many more muscle groups. An additional feature of opening-grasping is that central neural structures implicated in the control of this component have been homologized with (pyramidal) structures involved in the neuromotor control of mammalian distal musculature (Levine and Zeigler, 1982).

Opening-grasping is therefore a stereotyped response component of eating that is easily elicited under controlled conditions, and is readily quantifiable in terms of both stimulus and response variables. Furthermore, it is controlled by a simple muscle system.

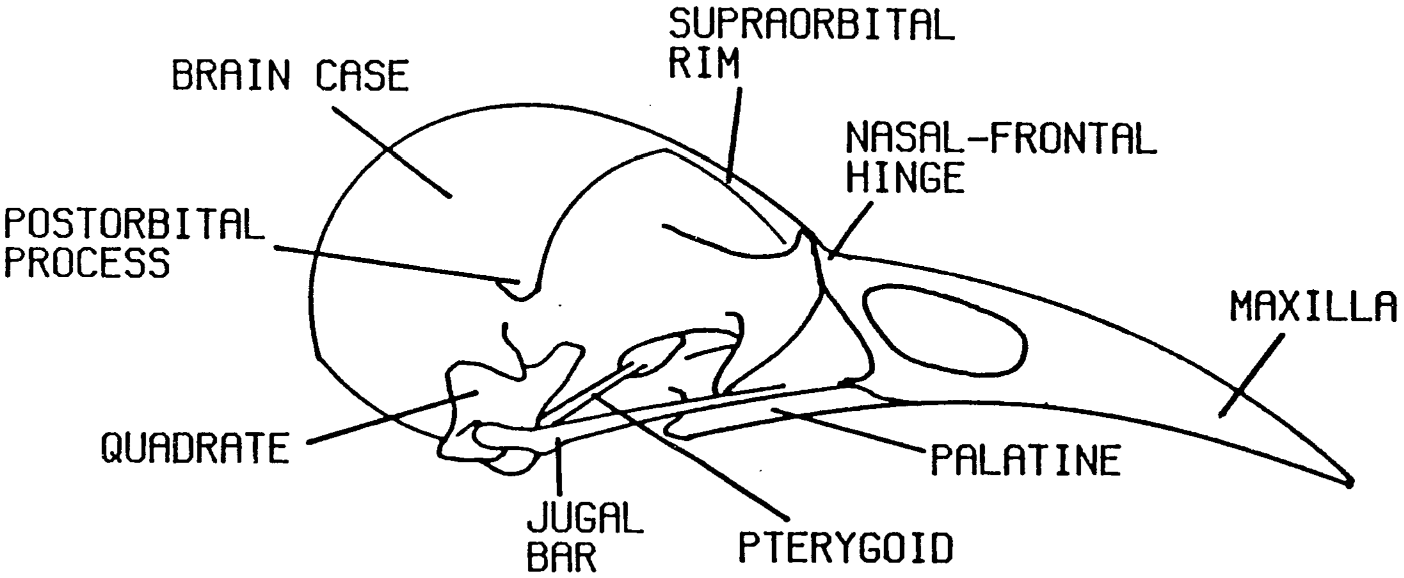
As noted above, a systematic neurobehavioral analysis should begin at the periphery, with the overt behavior. The first part of this dissertation therefore provides a description of the topography and spatiotemporal organization of the opening-grasping component of eating in the pigeon. Using high speed photography, the organization of jaw movements during opening-grasping are examined, as well as the behavioral mechanisms accounting for the adjustment of gape to seed size. The second part of the dissertation attempts to identify the final common path for opening-grasping by sectioning the motor nerves which innervate the jaw opener muscles, and determining the effect upon the response.

Experiment 1- Topography and spatiotemporal organization of opening-grasping.

A prerequisite for understanding the neural control of opening-grasping is a description of the topography and spatiotemporal organization of this response component. Such a description, combined with a knowledge of cranial morphology, may provide clues regarding the muscular control of the response. Knowledge of the muscle control of the response, in turn, indicates where an analysis of efferent neural control should begin. Furthermore, a behavioral description of opening-grasping will provide baseline data for studies involving neural manipulations (eg. denervation or lesion). In order to determine the questions which should be addressed by a description of opening-grasping, one must first understand the morphology of the grasping apparatus.

Morphological considerations. The avian skull can be divided into several major functional units. These are: 1) the brain case, 2) the upper jaw or maxilla, 3) the lower jaw or mandible, 4) the bony palate and 5) the quadrate (Bock, 1964) (see Figure 1). Components 2 through 5 are moveable with respect to the brain case. The ability of the upper jaw (maxilla) to move relative to the brain case is referred to as cranial kinesis. It

Figure 1. Lateral view of the avian skull (drawn from Bock, 1964). The mandible (not shown) can be seen in Figure 4.


SUPRAORBITAL RIM
BRAIN CASE
NASAL-FRONTAL HINGE
POSTORBITAL PROCESS
MAXILLA
QUADRATE
PALATINE
JUGAL BAR
PTERYGOID

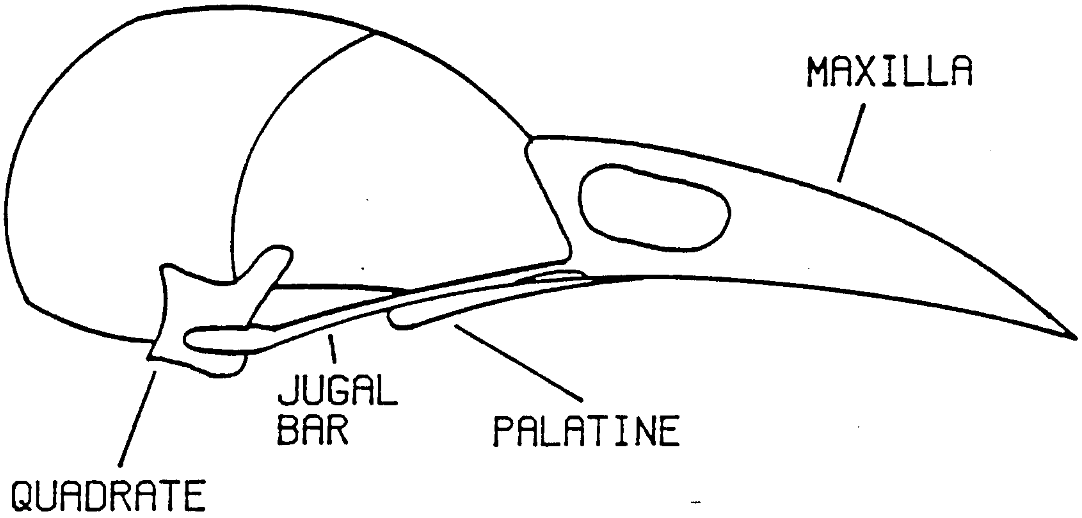
is a property absent in mammals, present in all birds and shared by some of the reptiles, fishes and fossilized amphibians.

Cranial kinesis would not be possible without the presence of a hinge around which the maxilla can rotate. In the pigeon, this structure is the naso-frontal hinge, a flexible strip of bone located at the junction of the maxilla and the brain case (see Figure 1). Rotation about the naso-frontal hinge is referred to as prokinesis (Bock, 1964).

The quadrate also plays a major role in kinesis by virtue of its ability to rotate around its articulation at the ventrolateral corner of the braincase. Manipulation of boiled skulls or those from freshly killed birds show that when the quadrate moves forward, the maxilla is raised by a series of bony struts (see Figures 2 & 3). The ventromedial portion of the maxilla is connected to the quadrate by the palatine-pterygoid bars, while the ventrolateral portion is connected to the quadrate by the jugal bars. Functionally, this strut system can be considered a single unit, with applied force resulting in an upward rotation of the maxilla about the naso-frontal hinge (Bock, 1964).

The protractor quadrati muscle originates from the postero-internal angle of the orbit and inserts upon the body of the quadrate, and on the head of the

Figure 2. The maxilla at rest (top), and during protraction as the quadrate rotates forward (bottom).


MAXILLA
JUGAL BAR
PALATINE
QUADRATE

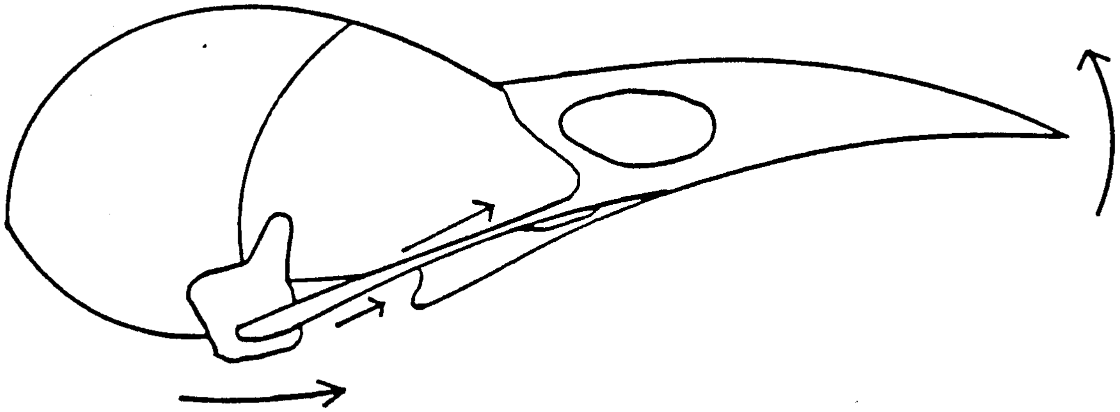
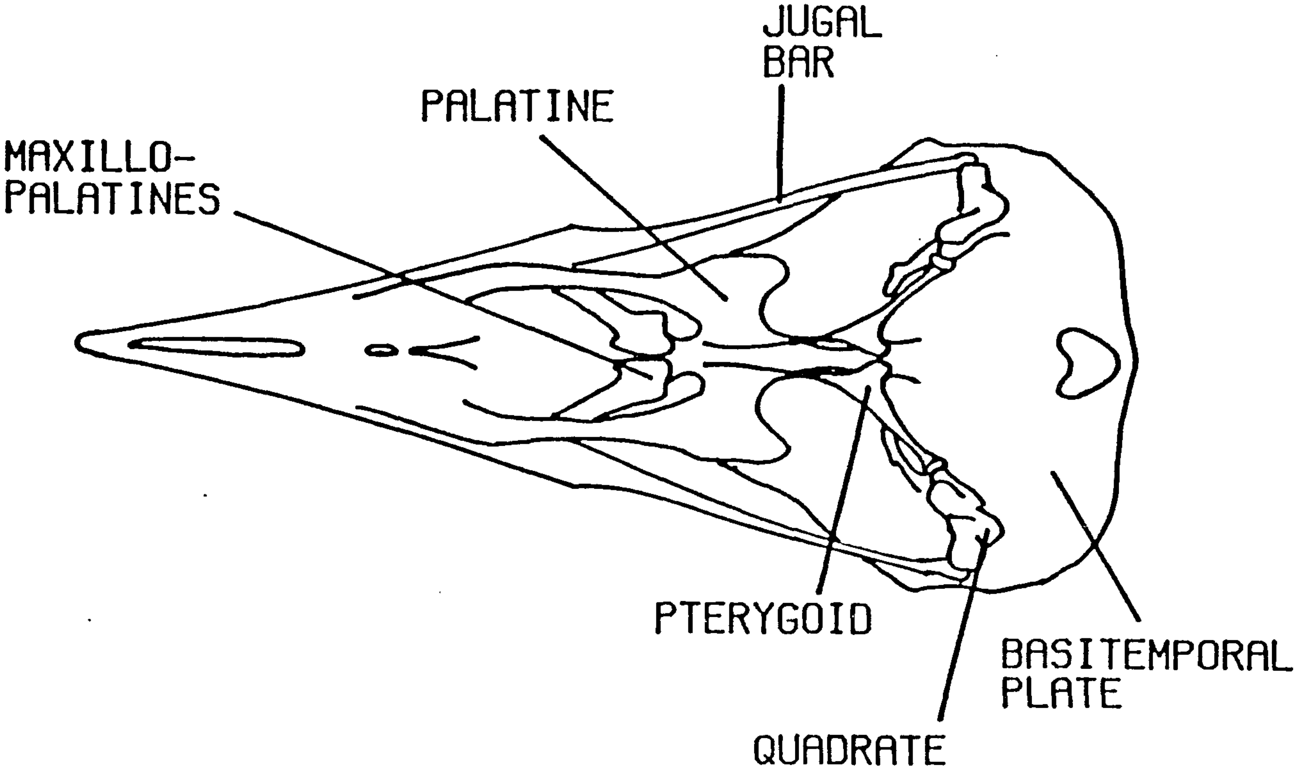


Figure 3. Ventral view of the avian skull showing the bony struts (pterygoids and jugal bars) involved in raising the maxilla (drawn from Bock, 1964).


JUGAL BAR
PALATINE
MAXILLO-PALATINES
PTERYGOID
BASITEMPORAL PLATE
QUADRATE

pterygoid where it articulates with the quadrate (see Figure 4) (Beecher, 1951). This muscle can supply the force for maxillary protraction. When M. protractor quadrati contracts, the quadrate swings forward, raising the maxilla by the mechanism outlined above (Bock, 1964).

The mandible, or lower jaw, is bound to the ventral end of the quadrate, and can rotate about this articulation. The force for mandibular depression (lowering) is provided by the depressor mandibulae muscle, which originates from the occipital plate of the brain case and inserts upon the retroarticular and internal processes of the mandible (see Figure 4). The lower jaw is also an area of attachment for the jaw closer muscles (M. pterygoideus, M. pseudotemporalis profundus, M. pseudotemporalis superficialis and M. adductor mandibulae) and various ligaments (see Figure 5). These ligaments serve several purposes, such as protecting the quadrato-mandibular articulation from detachment (eg. internal and external jugomandibular ligaments), and preventing excessive movement of the upper jaw (eg. occipitomandibular ligament). The post-orbital and lacrymomandibular ligaments run from the brain case to the external process of the mandible. The presence or absence of these ligaments is a major factor in determining the mechanism for cranial kinesis.

There are two basically different mechanisms of

Figure 4. The origin and insertion of the jaw opener muscles (protractors) of the pigeon (drawn from Wild and Zeigler, 1980). M.PQ = M. protractor quadrati, M.DM = M. depressor mandibulae.

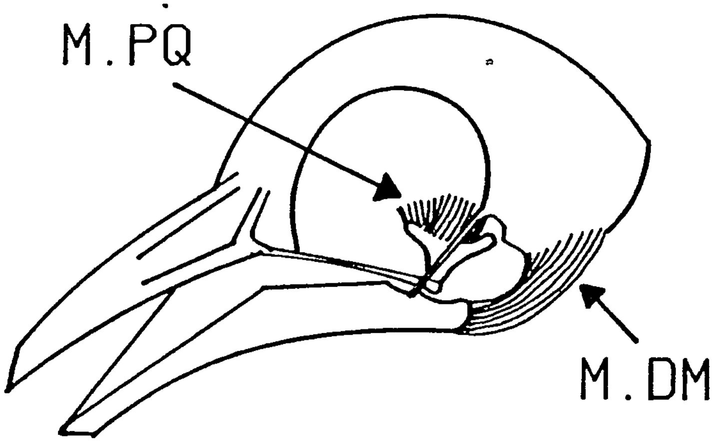
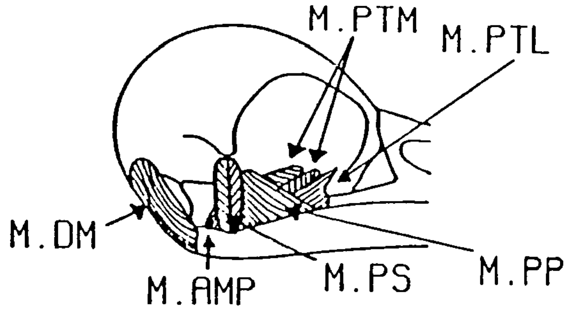
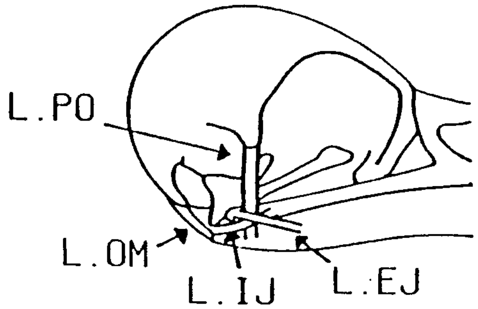

M.PQ
M.DM

Figure 5. Muscles (top) and ligaments (bottom) with attachments to the mandible (drawn from Bock, 1964). M.PTM = M. pterygoideus medialis, M.PTL = M. pterygoideus lateralis M.PS = M. pseudotemporalis superficialis, M.PP = M. pseudotemporalis profundus, M.AMP = M. adductor mandibulae posterior, M.DM = M. depressor mandibulae. L.PO = post-orbital ligament, L.OM = occipitomandibular ligament, L.IJ = internal jugomandibular ligament, L.EJ = external jugomandibular ligament.


M.PTM
M.PTL
M.DM
M.AMP
M.PS
M.PP


L.PO
L.OM
L.IJ
L.EJ

kinesis, uncoupled and coupled (Bock, 1964). Uncoupled kinesis is characteristic of those few birds which lack, or possess vestigial forms of, the post-orbital and lacrymomandibular ligaments (eg. the carduellne, and some cardinaline finches). In these species, the jaws are mechanically independent of one another. Movements of the mandible have no effect upon movements of the maxilla and vice versa. Opening of both jaws in uncoupled kinesis therefore always involves two separate mechanical actions.

Coupled kinesis is characteristic of those groups which possess a post-orbital or lacrymomandibular ligament. In these animals, there is a mechanical linkage between the jaws, such that contraction of M. depressor mandibulae may (under certain conditions) result in a corresponding raising of the maxilla. The following description of how this could occur mentions only the post-orbital ligament.

The post-orbital ligament runs from the post-orbital process of the brain case to an area of the mandible just anterior to the quadrato-mandibular articulation (see Figure 5). When M. depressor mandibulae contracts, the mandible tends to move downward. However, since the post-orbital ligament is inextensible, it prevents this movement and its insertion thereby becomes the fulcrum of a lever system. The force applied to this system by the contraction of M. depressor mandibulae, produces a resultant force which causes the quadrate to rotate around its articulation with the brain case. As the quadrate moves forward and upward, 1) the mandible is able to depress by pivoting around the mandibular attachment of the ligament (fulcrum) and 2) the upper jaw is raised.

In coupled kinesis, several modes of jaw opening are possible, depending upon the contraction sequence of the jaw opener muscles (Bock, 1964). In any mode, whenever the post-orbital ligament is loaded (taut), the mandible cannot be lowered without a corresponding raising of the upper jaw. 1) If only the protractor quadrati muscle contracts, the maxilla alone will be raised, with no assistance from M. depressor mandibulae. 2) If M. protractor quadrati contracts before M. depressor mandibulae both jaws will open, however, since the quadrate will be moving forward before the mandible begins to depress, the ligament will remain unloaded. Therefore, M. depressor mandibulae does not assist in raising the upper jaw. 3) If M. depressor mandibulae contracts prior to M. protrator quadrati, the ligament will become loaded as the mandible tends to move downward. The jaws will therefore open simultaneously, with the depressor mandibulae muscle playing a role in raising the maxilla. 4) Contraction of M. depressor mandibulae alone will also result in simultaneous opening of both jaws since the ligament will again (as in #3) become loaded.

Definitive determination of which of the above scenarios is operating would require measurements of structural movement, force and muscle activity (electromyogram). For example, a muscle may be contracting, yet produce no movement of a structure due to antagonistic forces upon that structure. Inferences based upon any one of these measurements are therefore somewhat limited without the other two.

Topographic organization of jaw movements during opening-grasping. The pigeon (*Columba livia*) possesses a well developed post-orbital ligament. Therefore, coupled kinesis is characteristic of this species. In order to address the mode of jaw opening that may be operating during grasping, the topographic organization of jaw movements will be described in terms of: 1) which jaws are opening and 2) in what order they open. Although this analysis of structural movement will be subject to the limitations noted above, it will represent an initial step toward an understanding of the events responsible for beak opening during seed grasping.

Given the fact that gape size varies with seed size (Zeigler, Levitt and Levine, 1980) it is important to determine whether the mode of jaw opening also changes. For example, maxillary protraction alone may occur for small seeds, while simultaneous opening of both jaws (yielding a larger final gape) may occur for larger seeds. The topography of jaw opening will therefore be examined over a range of seed sizes.

Mechanisms of adjusting gape to seed size. As noted above, gape size varies in a linear fashion with seed diameter. Since gape is adjusted prior to seed contact, the behavioral mechanisms responsible must operate during fixation, pecking or opening-grasping, and must ultimately influence the velocity of gape (the amount of beak opening per unit time), the duration (how long the beak opens) or both.

Decreasing the velocity of head descent as seed size increases would allow beak opening to occur over a longer period of time, thereby producing a larger gape by the time the beak reaches the level of the seed. Decreasing the latency of beak opening with respect to the start of head descent would also give the beak more time to open during head descent. Increasing the height above the seed at which head descent begins would have a similar effect as the two factors already discussed, and given a constant latency of beak opening, would result in an increase in the height at the start of beak opening.

Increasing the velocity of beak opening would also result in a larger gape by producing more gape per unit time of beak opening.

Determining which of these factors vary as a function of seed size will provide insights regarding which efferent systems are responsible for the gape function. Since the jaws are transported through space by movements of the neck (via the head), either of the systems controlling these structures can produce variations in the amount of gape generated during eating. If the velocity or latency of beak opening is important in gape adjustment, then the efferent system controlling the jaws would be implicated. On the other hand, if velocity of head descent or distance above the seed at the start of head descent is a significant factor, then the efferent system controlling the neck muscles would be implicated. Of course, such possibilities are not mutually exclusive and adjustment of gape may involve several of the factors listed above.

Method

Subjects

Five male White Carneaux pigeons (Columba livia), more than 5 years old and weighing 550 to 700 grams, were obtained from a commercial suppplier. They were housed individually, in a colony room, with a 15:9 light:dark cycle and an ambient temperature ranging from $21^{o}$to 27^{o}C. Prior to participation in the study, all birds were allowed at least one month to adapt to laboratory conditions during which time food and water were available ad libitum (ad lib). Weights were recorded 3 times per week.

Apparatus

High speed cinematography (400 frames per second) (fps) was carried out with a Hycam (Redlake Co.) 16 mm motion picture camera fitted with a Sony 12.5 to 75 mm zoom video lens. The camera body was placed in a styrofoam insulated wooden box in order to attenuate the sound of the camera motor. Kodak 16 mm Tri-X reversal black and white film (ASA 160-200) was used. Two 1000 W flood lights provided illumination, in addition to the ambient light of the room. A Gossen Pilot light meter was used to standardize the lighting conditions across filming sessions.

During filming, the birds ate from a Plexiglas feeder designed to fit on the home cage. This allowed the animals to remain in their cages during photography, minimizing the novelty of the filming situation. The left wall of the feeder was covered with white contact paper and served as a high contrast background for filming. The wall facing the camera was transparent. A V-shaped access space was cut from the wall which faced the cage. This prevented the birds from adopting undesirable feeding postures (eg. long axis of the body tilted towards or away from the camera), but did not otherwise alter normal feeding topography (determined by visual inspection). To maintain the seeds in a fixed configuration, the floor of the filming feeder was lined with white contact paper, sticky side facing up.

Prior to any behavioral procedures, a reference device (RD) was affixed to each animals skull. The device was comprised of two brass pins mounted in dental cement along the midline. The RD provided a fixed reference structure from which beak movements were measured.

For film analysis, a Leitz Prado Universal micro-projector with a 65 mm lens was used to project single frames onto an Apple Graphics Tablet. The tablet was interfaced with an Apple II microprocessor. Measurements made from the film were stored in data files on floppy disks for later processing.

Procedure

Mounting the RD. Animals were anesthesized with Chor-O-Pent (Fort Dodge Laboratories), 2 ml/kg of body weight, injected into the breast muscle. Supplementary doses of 0.2 ml were given whenever the bird responded to a toe pinch with vigorous foot withdrawal. After trimming head and ear feathers, the bird was mounted in a Kopf stereotaxic apparatus. The beaks rested on top of a rat mouth bar and were held in place by the nose clamp. A midline scalp incision was made and the skin flaps were reflected. The skull was then scraped clean of all remaining tissue and dried blood. A matrix of eight 1 mm burr holes was drilled in the area upon which the RD was to be mounted to insure that the dental cement would adhere to the skull. The head was then adjusted such that the axis running between the upper and lower jaws (in the closed position) was horizontal. Using an electrode carrier, the rostral pin of the RD was then lowered and cemented to the surface of the skull, on the midline suture, 20 mm posterior to the caudal edge of the cere. After 10 minutes drying time, the carrier was removed, and the caudal pin was affixed with its base 10 mm ventral and 10 mm caudal to the tip of the rostral pin. This insured that the pin tips had the same height, and that a line projected through them was parallel to the horizontal axis of the jaws. The electrode carrier was then removed, and any exposed areas of skull between the pins were covered with dental cement. After another 10 minutes of drying time, the skin flaps were closed around the RD with Ethicon 6-0 silk sutures. The wound was sprinkled with Neosporin powder and the animal was placed in the home cage to recover. The surgery lasted approximately 1.5 hours from the time of initial injection.

Feeder training and adaptation to the filming situation. Several factors made it necessary to insure that the birds would rapidly and reliably approach the feeder upon its presentation under filming conditions. These were, 1) rapid film speed (400 fps), 2) high film cost, and 3) a two second warm up period for the film to reach appropriate speed each time the camera was turned on. Training toward this goal began two days after recovery from the RD implantation procedure. The birds were deprived of food until they reached 85% of ad lib weight. Water remained continually available. Upon reaching the weight criterion, the daily food ration (15-20 g) was presented each day, in the filming feeder, for a maximum of 20 minutes. The ration consisted of a mixture of three seed types, milo (4.1 ± 0.8 mm), maple peas (7.0 ± 1.3 mm) and chick peas (garbonzo, 9.05 ± 1.01 mm) (values based on samples of 10 seeds each). If all the seeds were consumed the feeder was removed one minute after the last seed was eaten. If the animal failed to eat all the seeds within 20 minutes, the feeder was removed until the next days presentation. After 5 consecutive days of approaching the feeder within 2 sec and consuming all the seeds (adaptation criterion), the home cage was moved from the home rack to the filming stand for the feeding of the daily ration. In order to adapt the birds to camera noises (still audible from the sound attenuating container) and the high intensity flood lights, subsequent feeding was done with the flood lights on while the camera was turned on and off. These factors initially inhibited approach to the feeder, however, they did not appear to alter response topography (determined by visual inspection) once eating was initiated. When the animals reached the adaptation criterion under these conditions, the daily ration was subsequently presented one seed type at a time with order of seed types being random. In addition, a cardboard partition with a 6 foot string attached was placed in front of the opening of the feeder and pulled away to allow access to the food. The purpose of the partition was to allow the experimenter time to get back to the camera and turn it on before the seeds were consumed. By controlling access to the seeds, the camera could be run for a 2 sec warm up period before the bird began to feed. This insured that all feeding was filmed at 400 fps. Once adapted to removal of the partition, the birds were ready for filming.

Filming. On the day of filming, the home cage was placed on the filming stand and the bird was removed while adjustments of the camera, flood lights and cage were made. During this time, the animal remained in a plastic weighing tube. The distance of the cage from the camera was reproduced across filming sessions by using a piece of tape which extended 1.5 m from the film plane. The illumination level was reproduced across sessions by adjusting the position of the flood lights to produce the same light meter reading each time. The film speed (400 fps) was calibrated each session by adjusting the film speed dial until an exposed 4000 frame roll of film took 10 sec to run through the camera. After adjustments of the filming set-up were made, the brass pins of the animals RD were covered with 2 coats of black paint. This provided good contrast between the pins and the white filming background. In addition, a 0.5 mm spot of black paint was placed on both the maxilla and mandible, 3 mm from the tip and midway between the dorsal and ventral surface of each jaw. The spots were clearly visible against the pink background of the jaws. These markers (black pins and black spots) were later used in the analysis of the films (see Data analysis). The animal was then placed back into the cage and the flood lights were turned on. Seeds were presented one type at a time, in random order. Each set of seeds presented was arranged in 2 staggered rows down the center of the feeder. The feeder was then placed onto the front of the cage with the cardboard partition blocking access to the seeds. After the camera was turned on for approximately 2 sec, the partition was pulled away and the animal was filmed as it ate. Each animal was filmed during the consumption of 2 sets of each seed type. All 3 seed types were presented once, before the second randomly selected set was presented.

Data Analysis

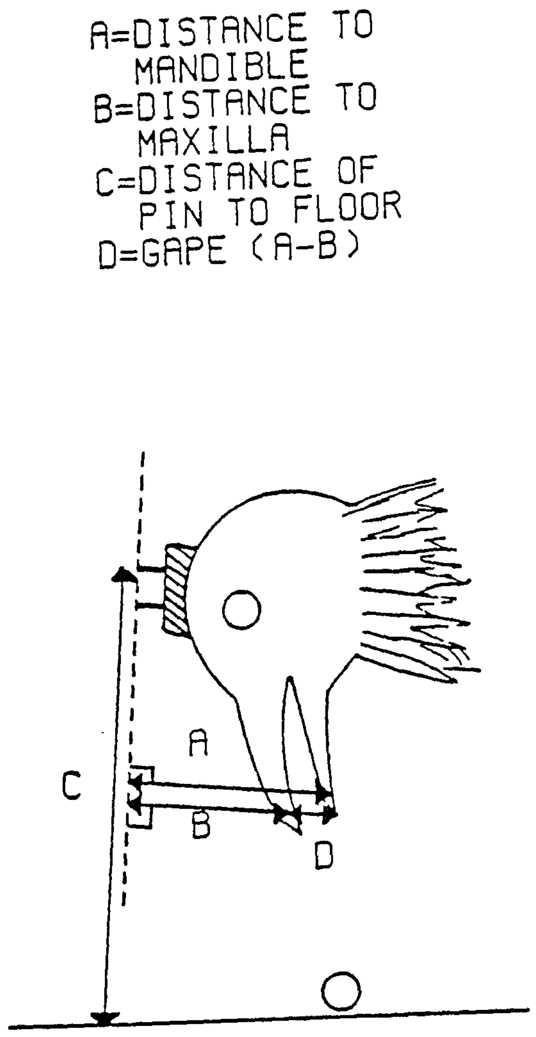
Preliminary review. Each roll of film was initially scanned at normal viewing speed (24 fps) in order to select eating sequences appropriate for frame-by-frame analysis. A sequence was chosen only if the sagittal plane of the head remained parallel to the film plane throughout the response.

Frame-by-frame analysis. Each acceptable eating sequence was analyzed backwards, beginning with the frame in which both beak tips were just above the top of the seed, but not touching it. This was termed frame zero and was chosen since 1) it assured that the seed would not produce a physical alteration of jaw opening topography and 2) jaw closing had not yet begun at this point. Frame zero and the previous 31 frames were analyzed since pecking and opening-grasping always occurred within this 75 msec interval.

Individual frames were projected onto the graphics tablet and (through appropriate microprocessor programming) measurements were made by pressing a stylus onto a set of predetermined points (see Figure 6). The features measured were: 1) position of the maxilla (with respect to the RD), 2) position of the mandible, 3) gape, and 4) position of the head with respect to the substrate. Each frame was analyzed 4 times, and the mean of these measurements was recorded on a floppy disk. This frame-by-frame procedure provided a spatiotemporal description of individual jaw and head movements during pecking and opening-grasping.

Error estimate. In order to determine the precision of measurement, the above procedure was repeated 32 times on the same frame (4 replicates performed 32 times). After each set of 4 replicates, the frame was moved to a slightly different position on the graphics tablet in order to simulate the random change in frame position which occurred during normal frame-by-frame analysis.

Figure 6. Measurements made for each frame of a grasping sequence. The dashed line was calculated by the measurement program, and runs through the tips of the reference device.


A=DISTANCE TO
MANDIBLE
B=DISTANCE TO
MAXILLA
C=DISTANCE OF
PIN TO FLOOR
D=GAPE (A-B)
A
C
B
D

For each of the above features (gape, etc.), the mean and standard deviation of the 32 values (recorded on disk) was determined. The coefficients of variation were as follows: position of maxilla- 3.21, position of mandible- 2.47, gape- 5.47 and head position- 0.39.

The error in jaw position measurements produced by lateral rotations of the head (not detected during preliminary review of the films) was also estimated. To estimate the amount of lateral head rotation which might have gone undetected, a rectangular piece of metal (50 mm long X 20 mm wide) was held parallel to the coronal plane of the author's head and slowly rotated towards him until a change in position was detected. This process was repeated 5 times. The lateral rotation values which were just noticeable by the author ranged between 10° and 20° (measured with a protractor). The effect of rotations of this magnitude upon jaw position measurements was then estimated. The tips of a compass were used to simulate the distance between the tip of a jaw and the line projected through the ends of the RD (see Figure 6, distance B). Since a given lateral rotation of the head might result in a similar rotation of this RD-jaw tip distance (depending upon the axis around which the head is pivoting), the compass was rotated through a 20° arc. A 10° rotation of the compass produced a 2% decrease in the estimate of inter-compass tip distance, while a 20°

rotation resulted in a 6.5% decrease. Therefore, undetected lateral rotations of the head could have produced, at most, about a 6.5% error in the measurement of jaw position.

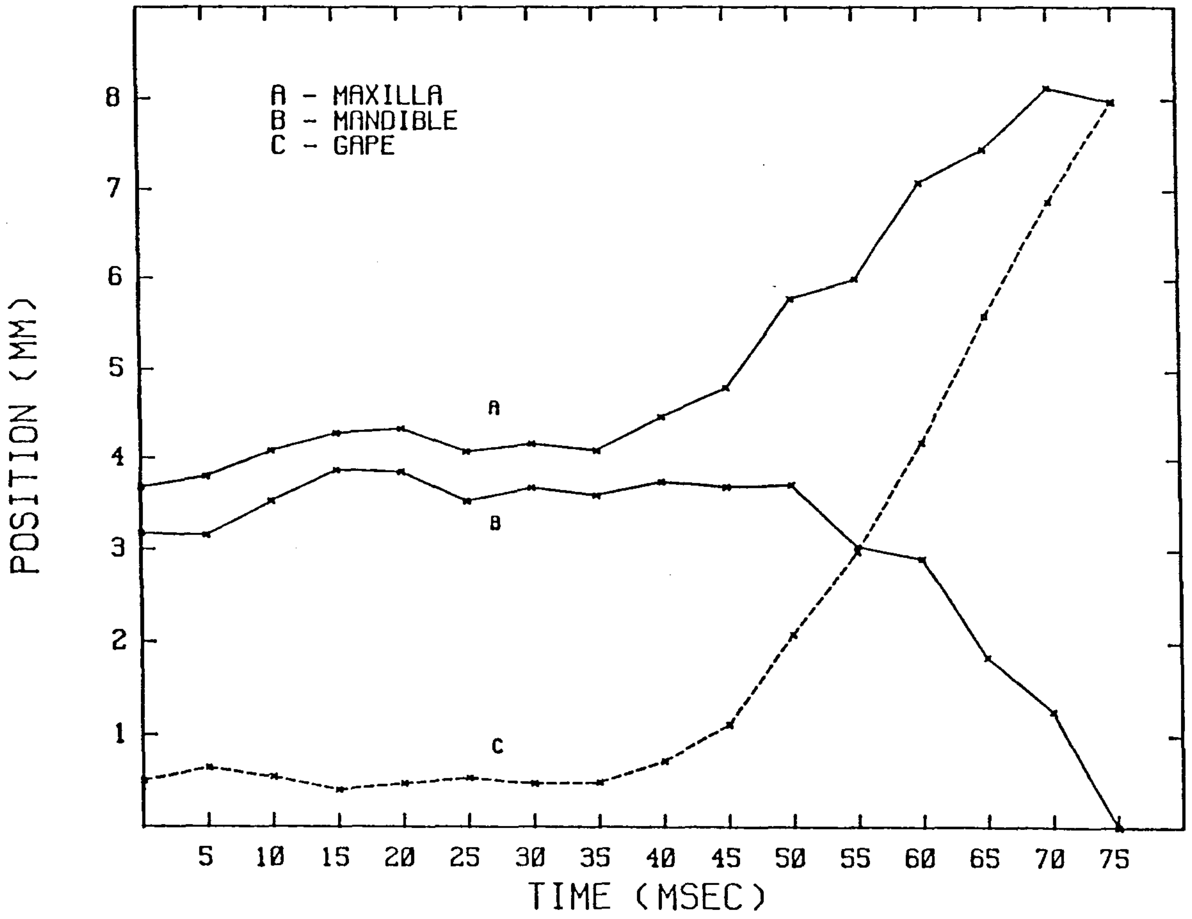
The geometric distortion introduced by the lens was also measured. While looking through the viewfinder, a pencil point was lowered toward a horizontal line drawn at the center of the field of view. A mark was made where it appeared to touch the line, and the distance from the line was measured. The process was repeated for a horizonal line 50 mm below the center, at the ventral border of the field of view. The difference between the 2 measured distances (of the pencil point from the line) was the geometric distortion, and was less than 1 mm. All measurements were made 1.5 m from the film plane, where the pigeon's head would have been.

Other sources of error could not be easily quantified. For example, the clarity of the RD tips sometimes appeared to change from frame to frame. This may have been caused by a change in the illumination of the RD tips as the head descended toward the substrate. For every eating sequence, the measurements for each 2 consecutive frames were averaged (forming a single measurement block) in an attempt to statistically control for such random sources of error.

Criterion for the start of mouth opening. To determine which jaws opened and in what order, it was necessary to establish the positions of the maxilla and mandible at the start of mouth opening. A criterion was therefore needed to determine when mouth opening began. This criterion was also needed to measure those characteristics noted above which may be contributing to the adjustment of gape to seed size (eg. velocity of mouth opening, etc.). Figure 7 is a plot of maxilla position (A), mandible position (B), and gape (C) over the course of a single response. The gape curve is generally flat prior to mouth opening and increases in a linear fashion after mouth opening begins. A frequency distribution of block to block changes in gape was compiled for the flat part of the gape curve (prior to mouth opening). Visual inspection revealed these changes to be distributed in an approximately normal fashion with only 2.5% exceeding 0.25 mm. Gape changes greater than 0.25 mm were therefore considered real, and those less than or equal to this value were considered error. The beginning of mouth opening was defined as the block preceeding the first gape change greater than 0.25 mm.

Criterion for the start of head descent. In order to properly assess the method used to adjust gape to seed size, a criterion was needed for determining the start of

Figure 7. Position of the maxilla, position of the mandible and gape, over the course of a single grasping sequence.


A - MAXILLA
B - MANDIBLE
C - GAPE
A
B
C
POSITION (MM)
1
2
3
4
5
6
7
8
TIME (MSEC)
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75

head descent. This was computed in the same fashion as the criterion for the start of mouth opening. Only 2.5% of the block to block changes in head position exceeded 0.50 mm. Therefore, the beginning of head descent was defined as the block preceeding the first change in head position (toward the substrate) greater than 0.50 mm.

Results

Organization of jaw movements

A total of 244 opening-grasping sequences (7808 frames) were analyzed. Table 1 shows the breakdown of sequences by bird and seed type.

To determine whether each bird opened the maxilla and mandible for each seed type, the change in position (displacement) of each jaw (from the start of mouth opening to frame zero) was calculated for each opening-grasping sequence. The mean of these change scores was then derived for the maxilla and mandible of each bird, under each seed type. A one-tailed dependent measures t-test was performed on each of the mean change values to test whether or not they were different from zero. The mean and standard deviation of the change scores are presented (see Table 2) for each jaw of each bird under each seed type, in addition to the value of the t-statistic. For the maxilla, a positive value represents upward movement and for the mandible a positive value reflects downward movement. Since 30 t-tests were performed, the significance level used in each was 0.001. This kept the probabilty of one or more type I errors at 3%. The anaysis showed that for every bird, under every seed type, the change in position of each jaw was greater than zero. Therefore, every bird

Table 1. Number of opening-grasping sequences analyzed by bird and seed type.

Bird #	Seed		
	Milo	Pea	Garbonzo
490	14	12	8
766	29	13	17
770	21	19	15
773	24	17	13
776	17	17	8

Table 2. Mean change in position (in mm) of the maxilla and mandible during opening-grasping, for each bird, under each seed type. The standard deviation and *t* statistic for these mean changes is also presented. MX = maxilla, MD = mandible.

Bird #	Seed								
	Milo			Pea			Garbonzo		
	$\bar{D}$	SD	t(df)	$\bar{D}$	SD	t(df)	$\bar{D}$	SD	t(df)
490	MX- 2.69	1.09	9.28(13)	MX- 3.05	1.07	9.84(11)	MX- 3.20	0.73	12.44(7)
	MD- 1.91	1.12	6.38(13)	MD- 3.06	1.31	8.10(11)	MD- 6.39	1.29	14.07(7)
766	MX- 2.53	0.48	28.61(28)	MX- 2.62	1.18	8.02(12)	MX- 3.53	0.99	14.69(16)
	MD- 1.65	0.82	10.86(28)	MD- 1.59	1.34	4.29(12)	MD- 2.46	0.98	10.31(16)
770	MX- 2.94	1.09	12.32(20)	MX- 3.33	0.75	19.25(18)	MX- 4.01	0.89	17.38(14)
	MD- 2.25	1.00	10.35(20)	MD- 2.07	1.16	7.77(18)	MD- 3.32	1.52	8.46(14)
773	MX- 2.53	0.81	15.22(23)	MX- 2.80	0.88	13.07(16)	MX- 3.03	1.17	9.33(12)
	MD- 0.78	1.01	3.80(23)	MD- 2.26	0.85	10.92(16)	MD- 2.52	1.21	7.51(12)
776	MX- 1.87	0.78	9.94(16)	MX- 3.12	0.85	15.16(16)	MX- 3.16	1.09	8.22(7)
	MD- 1.58	0.83	7.90(16)	MD- 1.47	0.96	6.34(16)	MD- 4.52	1.21	7.51(12)

was opening its maxilla and mandible for each seed type.

Figures 8 and 9 illustrate the effect of seed size upon the magnitude of opening of the maxilla and mandible, respectively, for each of the 5 birds. As seed size increases from 4.1 mm (milo) to 9.1 mm (garbonzo) all birds show an increase in the amount of displacement of each jaw. However, the fashion in which this increase occurs is more variable between birds in the case of the mandible. For the maxilla, all birds show a monotonic increase in displacement as seed size increases. With respect to the mandible, a monotonic increase in displacement (as seed size increases) occurs for 2 of the 5 birds. The other 3 birds show no increase in mandibular displacement as seed size increases from 4.1 mm to 7.0 mm (peas), followed by an increase in displacement as seed size increases from 7.0 mm to 9.1 mm.

A two-factor (2 jaws X 3 seed sizes) analysis of variance (ANOVA) with repeated measures on both factors was performed on the jaw displacement values presented in Figures 8 and 9. Seed size was found to have a significant effect upon the amount of jaw displacement (irrespective of jaw type) ($F(2,8) = 18.58$, $p < 0.05$). The displacement means and standard deviations (collapsed over jaw type) were as follows for milo, peas and garbonzo, respectively: 2.07 ± 0.64, 2.54 ± 0.66 and

Figure 8. Displacement of the maxilla during opening-grasping, as a function of seed size, for each of the 5 birds.

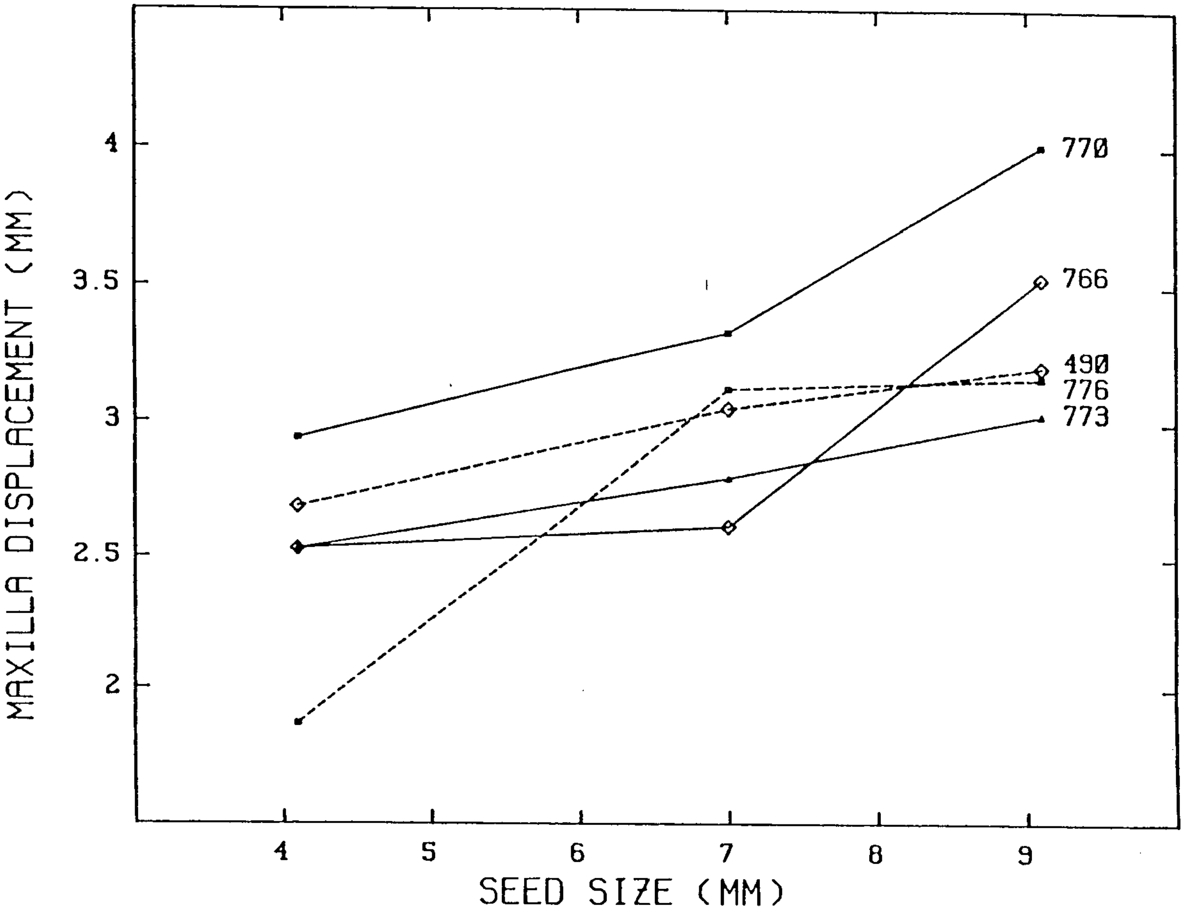
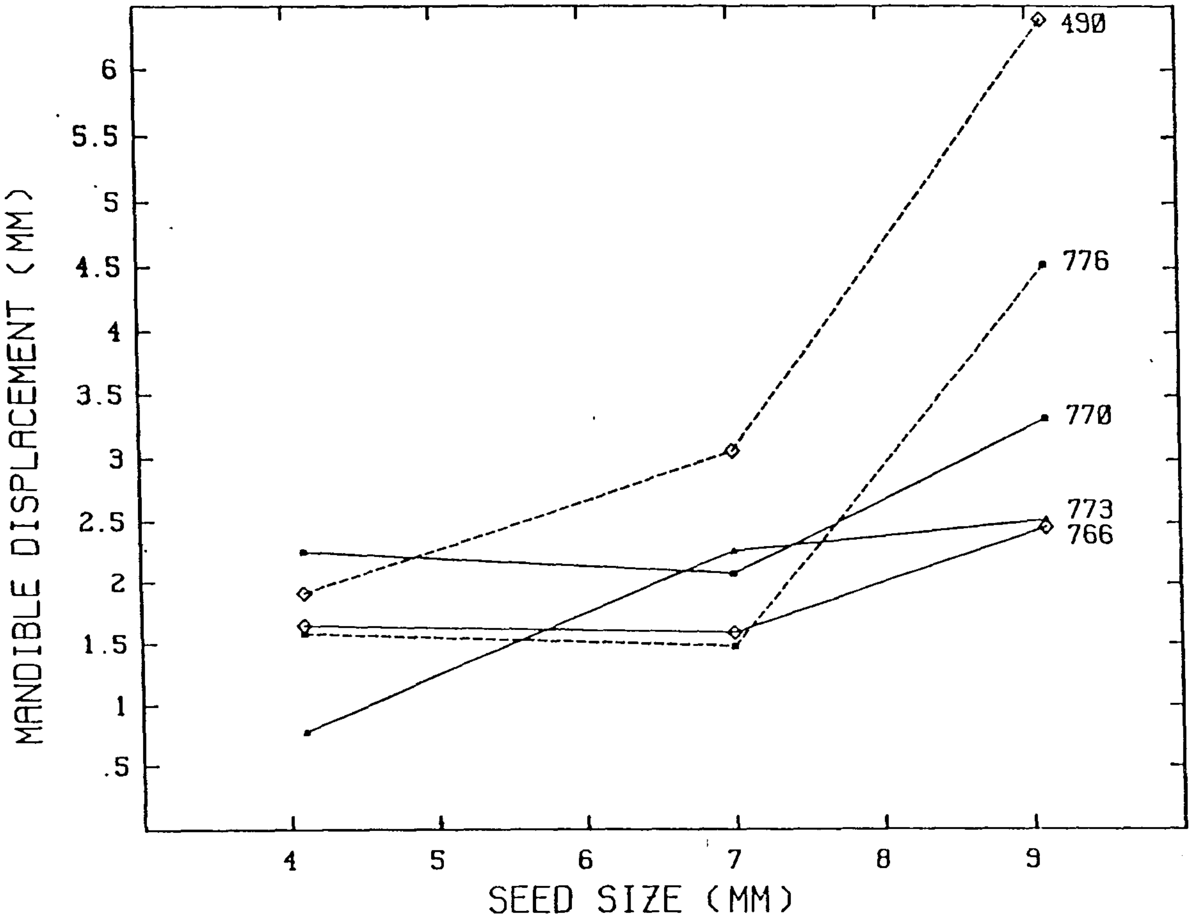

MAXILLA DISPLACEMENT (MM)
4
3.5
3
2.5
2
SEED SIZE (MM)
4
5
6
7
8
9
770
766
490
776
773

Figure 9. Displacement of the mandible during opening-grasping, as a function of seed size, for each of the 5 birds.

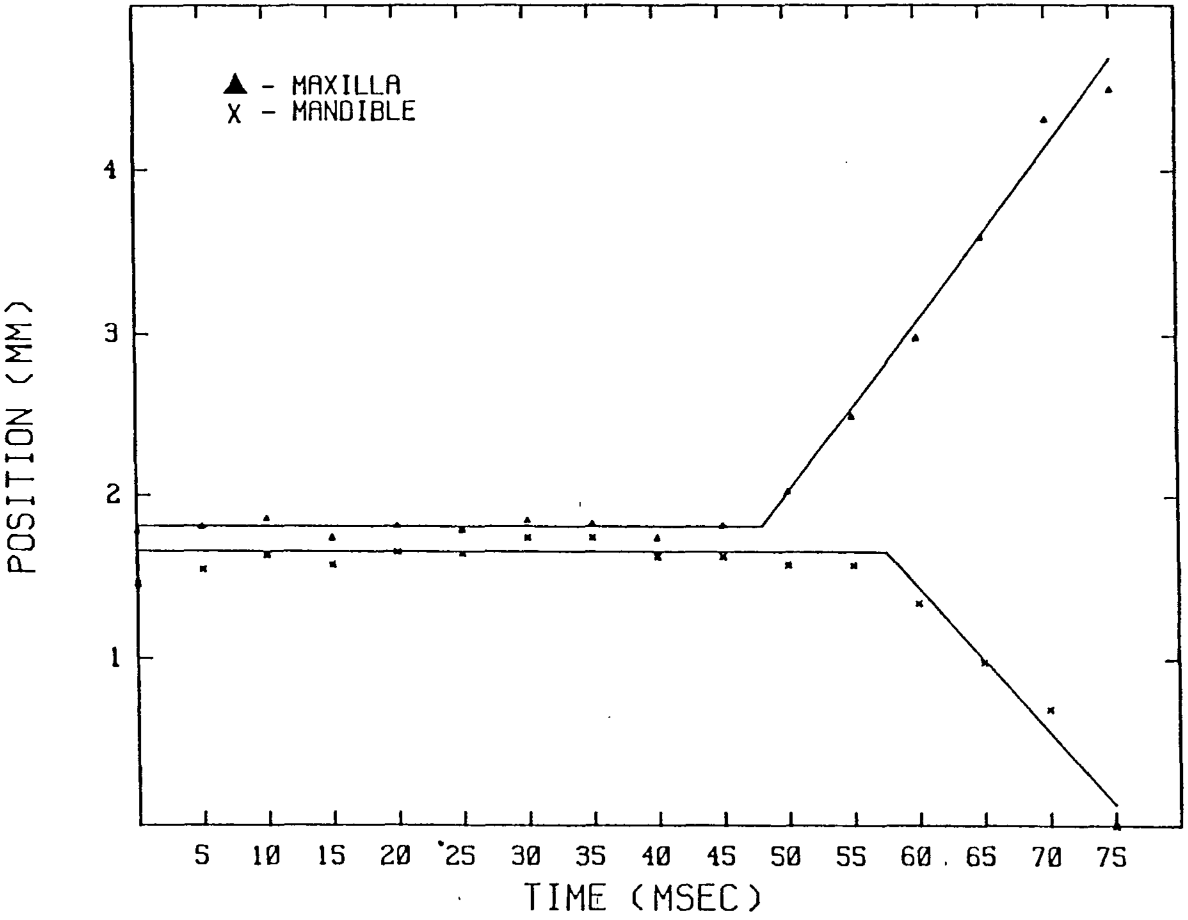


6
5.5
5
4.5
4
3.5
3
2.5
2
1.5
1
.5
MANDIBLE DISPLACEMENT (MM)
4
5
6
7
8
9
SEED SIZE (MM)
490
776
770
773
766

3.61 ± 1.16. No significant difference was found between the amount of displacement attributable to each jaw (irrespective of seed size) (F(1,4) = 1.63). Displacement means and standard deviations for the maxilla and mandible (collapsed over seed size) were 2.96 ± 0.50 and 2.52 ± 1.40, respectively. No significant interaction was found between jaw type and seed size (F(2,8) = 2.79). It therefore appears that: 1) the amount of jaw opening increases as a function of seed size, 2) the amount of opening attributable to the 2 jaws does not differ and 3) the effect of seed size upon jaw opening is not different for the 2 jaws.

To determine the order in which the two jaws opened, a modification of the non-linear regression procedure (NLIN) (SAS User's Guide, 1979) was used. The procedure assumes that the data conform to a segmented model with two linear portions, the first having a slope of zero and the second having either a positive or negative non-zero slope. Such a trend is illustrated by the solid lines in Figure 10. By varying 3 parameters, break point (point at which the slope changes from zero), slope and Y-intercept, a least squares fit of this model to the data is calculated. This procedure was used since individual jaw movements appeared to conform to the assumptions of the model (see Figure 7). The break point was used as an estimate for the start of opening of

Figure 10. Mean jaw position curves for the maxilla and mandible of a single bird (#766) consuming milo. Solid lines represent the least squares fit of each curve.


▲ - MAXILLA
X - MANDIBLE
4
3
2
1
POSITION (MM)
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
TIME (MSEC)

each jaw.

For each of the 5 birds the jaw (maxilla and mandible) position data for each opening-grasping sequence was averaged within each seed size. The NLIN procedure was then used to estimate the break point for each of these mean curves. For every curve, the least squares fit produced by NLIN accounted for more than 99.98% of the total variance. Figure 10 represents the mean jaw position curve for milo, with its corresponding least squares fit, for a single bird. The difference between the estimates of mandibular and maxillary opening latency are presented in Table 3, for each bird under each seed type. A one-way ANOVA with repeated measures revealed no significant effect of seed size upon these latency differences. The 5 scores for each of the 3 seed sizes were therefore considered a single set of 15 scores when examined with respect to direction of the latency difference. In 14 out of 15 comparisons, upper jaw opening preceded lower jaw opening. Assuming an equal probability of one jaw preceding the other (which would be the case if there were no difference in opening latency between the maxilla and mandible), the two-tailed binomial probability of obtaining 14 or more differences in the same direction is less than 0.001. The hypothesis that there is no difference in opening latency between the two jaws was therefore rejected. Therefore, opening

Table 3. Difference between the estimates of maxillary and mandibular opening latencies (in msec) for each bird, under each seed type. Positive values represent maxillary protraction preceding mandibular depression.

Bird #	Seed		
	Milo	Pea	Garbonzo
490	21.85	21.77	16.22
766	9.51	12.87	7.76
770	-2.36	3.41	8.02
773	10.25	4.63	6.95
776	4.66	6.30	2.46

of the maxilla was found to precede opening of the mandible.

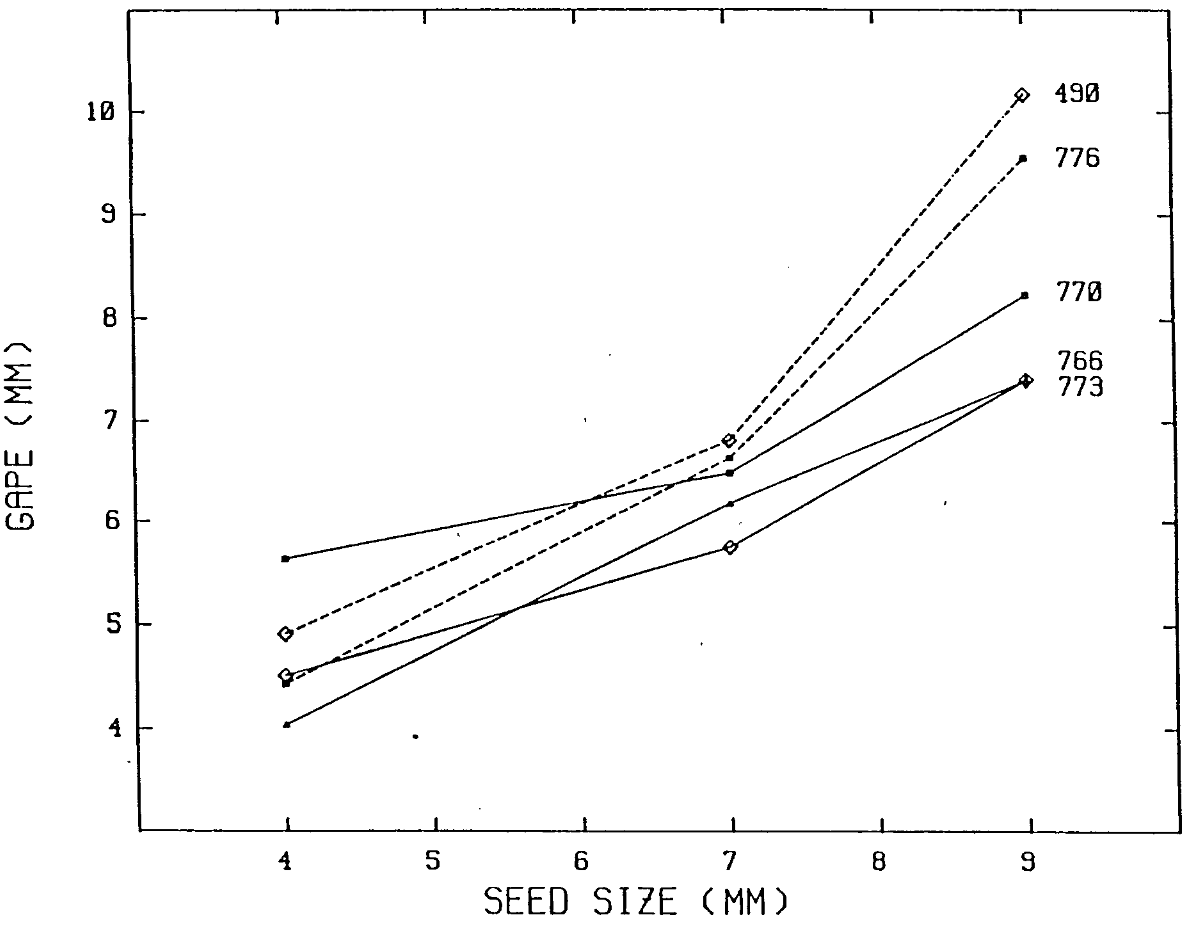
For a single bird (#766), 10 opening-grasping sequences for each seed type were randomly selected. The NLIN procedure was then used to estimate the break point for each jaw position curve (maxilla and mandible) of each response. The difference between the estimates of mandibular and maxillary opening latency was then determined for each opening-grasping sequence. The mean latency differences (and their corresponding standard deviations) were as follows for milo, peas and garbonzo, respectively: 16.2 ± 10.8, 11.6 ± 7.0 and 7.7 ± 13.7. As in the analysis of average opening-grasping curves for bird #766 (see Table 3), the mean opening latency differences (based on the analysis of individual opening-grasping sequences) for this animal were positive for all 3 seed sizes (opening of the maxilla preceding that of the mandible). Furthermore, the mean latency differences for peas and garbonzo were quite close to those in Table 3 (for bird #766), while the mean latency difference for milo was somewhat greater than the value determined by analysis of the average curve. A one way ANOVA on the mean opening latency differences for #766 revealed no significant effect of seed size (F(2,27) = 1.5). Twenty-six of the 30 sequences examined showed upper jaw opening preceding that of lower jaw opening.

The binomial probability (two-tailed) of obtaining 26 or more differences in the same direction was less than 0.001. The hypothesis that there is no difference in opening latency between the two jaws was therefore rejected. It appears that the analysis of opening latency differences for individual responses of a single bird were similar in both direction and magnitude to those values determined by the analysis of average curves for each seed size (see Table 3). Moreover, the conclusion with respect to the order of jaw opening in this bird was similar to the conclusion drawn for all birds based on the analysis of average curves.

Mechanisms of gape adjustment

For every eating response examined, the values of the following characteristics were determined: 1) gape, 2) velocity of mouth opening, 3) duration of mouth opening, 4) latency of mouth opening, 5) velocity of head descent and 6) distance from the seed at the start of head descent. All velocity measurements were calculated as total distance divided by total duration (average velocity), unless otherwise indicated. The mean value of each factor (across eating responses) was then determined for each seed size for each of the 5 birds, as well as across the 5 birds (mean functions). These data are illustrated in Figures 11 through 22. A one-way analysis

Figure 11. Gape as a function of seed size for each of the 5 birds.



490
776
770
766
773
10
9
8
7
6
5
4
GAPE (MM)
4
5
6
7
8
9
SEED SIZE (MM)

Figure 12. Gape as a function of seed size across all birds.

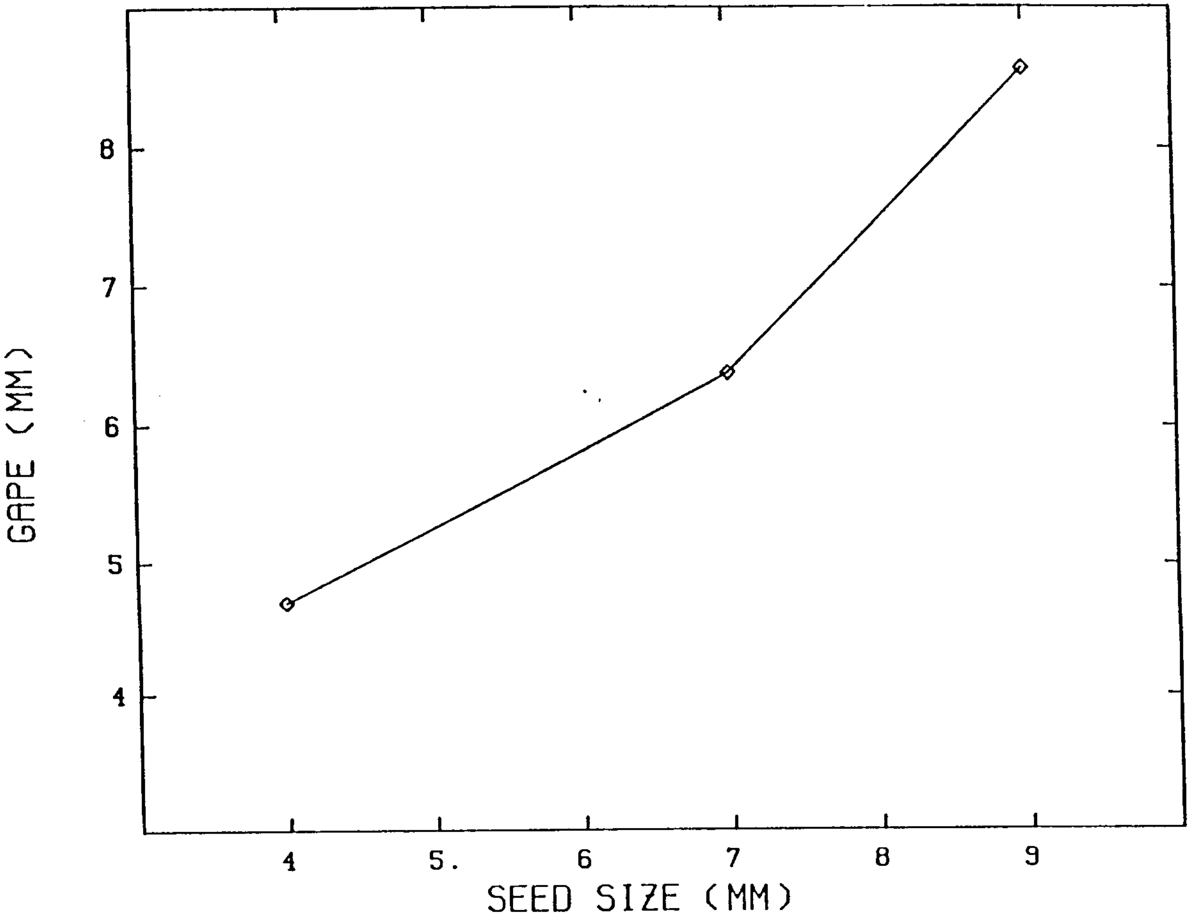

GAPE (MM)
8
7
6
5
4
4
5.
6
7
8
9
SEED SIZE (MM)

Figure 13. Velocity of mouth opening as a function of seed size for each of the 5 birds.

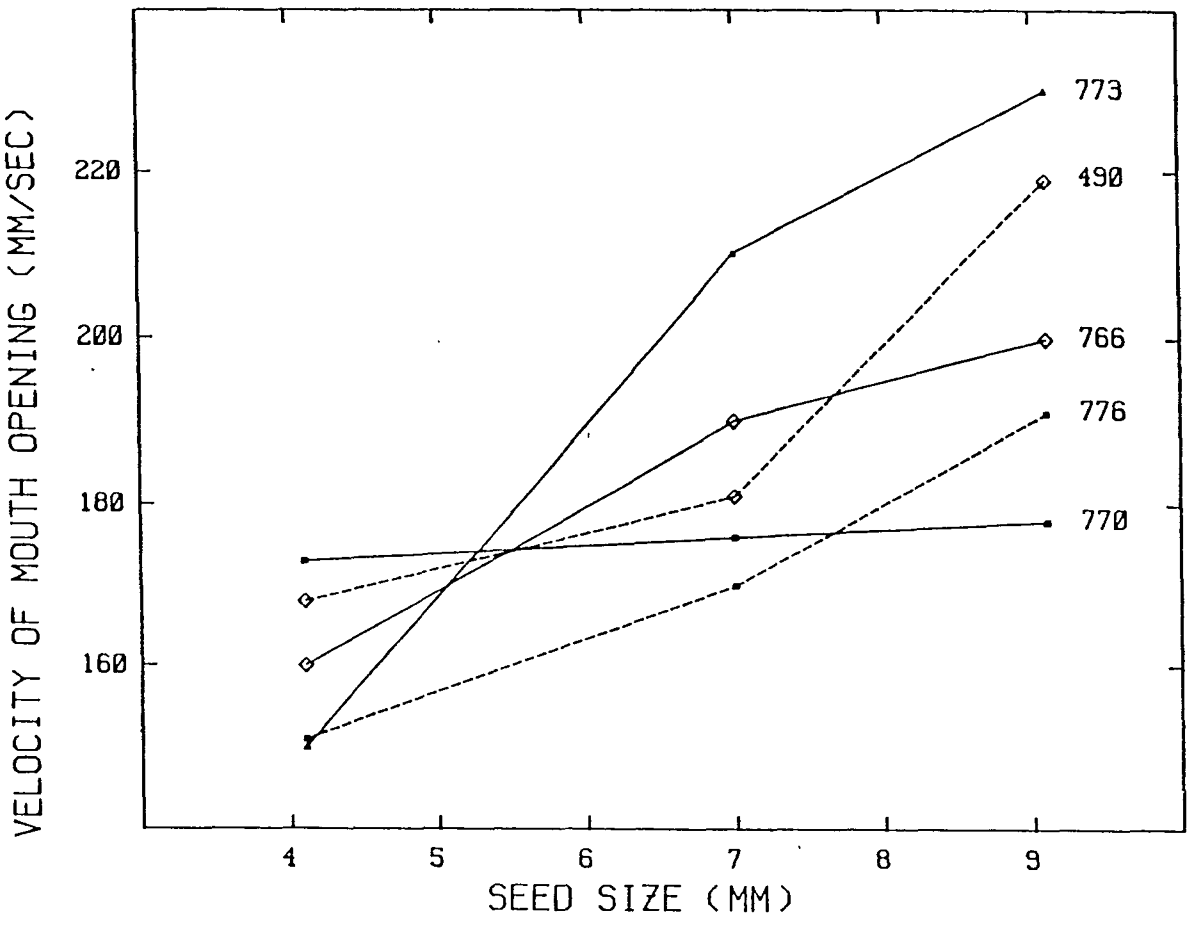

VELOCITY OF MOUTH OPENING (MM/SEC)
220
200
180
160
4
5
6
7
8
9
SEED SIZE (MM)
773
490
766
776
770

Figure 14. Velocity of mouth opening as a function of seed size across all birds.

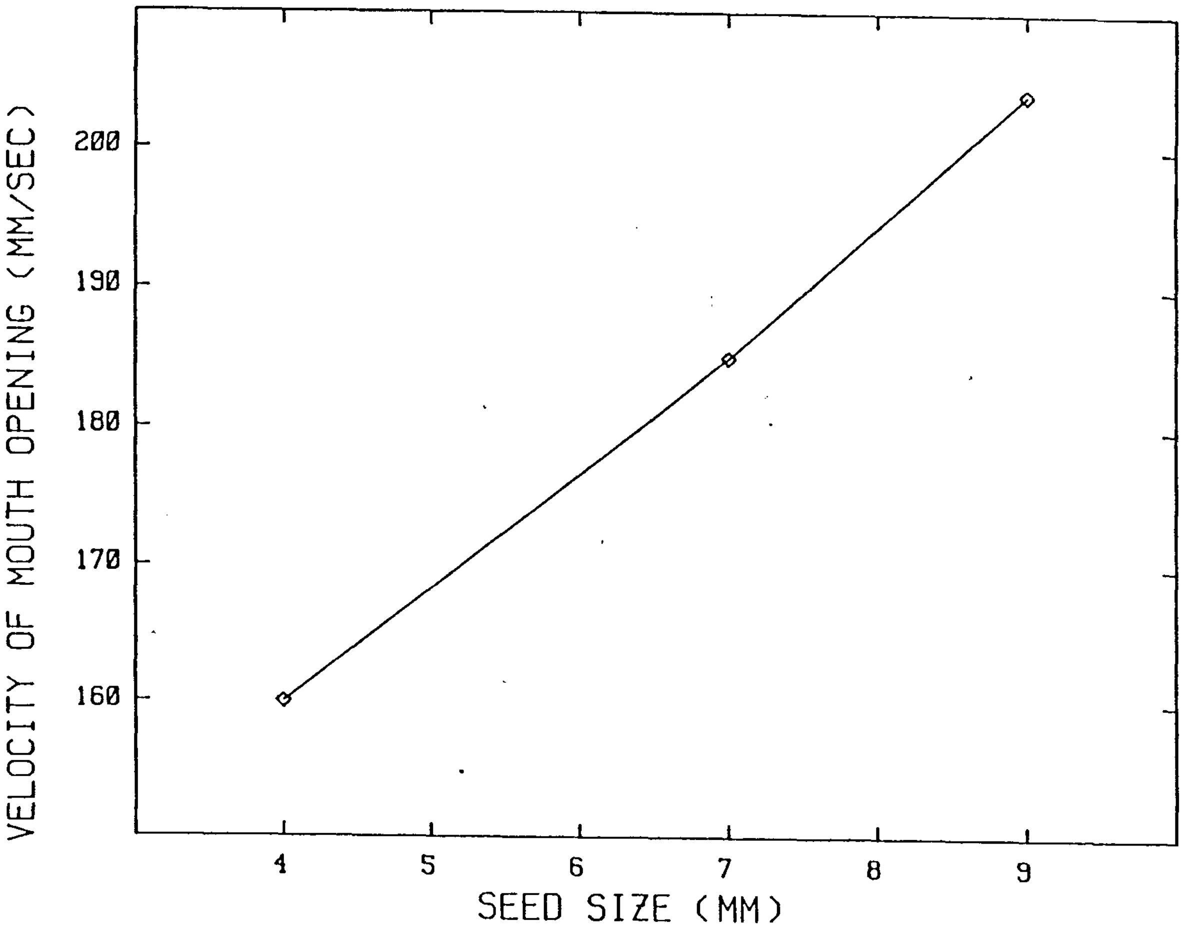

VELOCITY OF MOUTH OPENING (MM/SEC)
160
170
180
190
200
4
5
6
7
8
9
SEED SIZE (MM)

Figure 15. Duration of mouth opening as a function of seed size for each of the 5 birds.

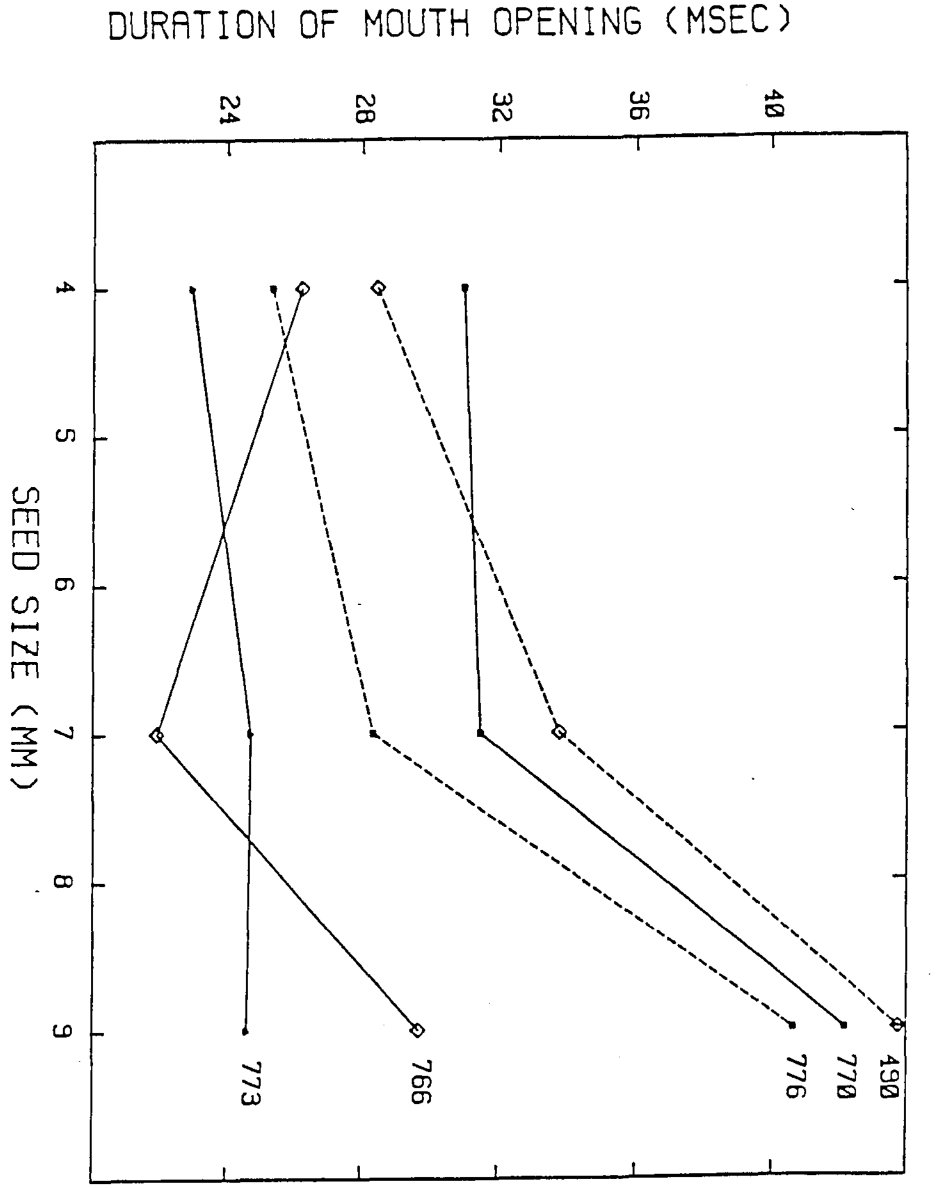

DURATION OF MOUTH OPENING (MSEC)
24
28
32
36
40
SEED SIZE (MM)
4
5
6
7
8
9
490
770
776
766
773

Figure 16. Duration of mouth opening as a function of seed size across all birds.

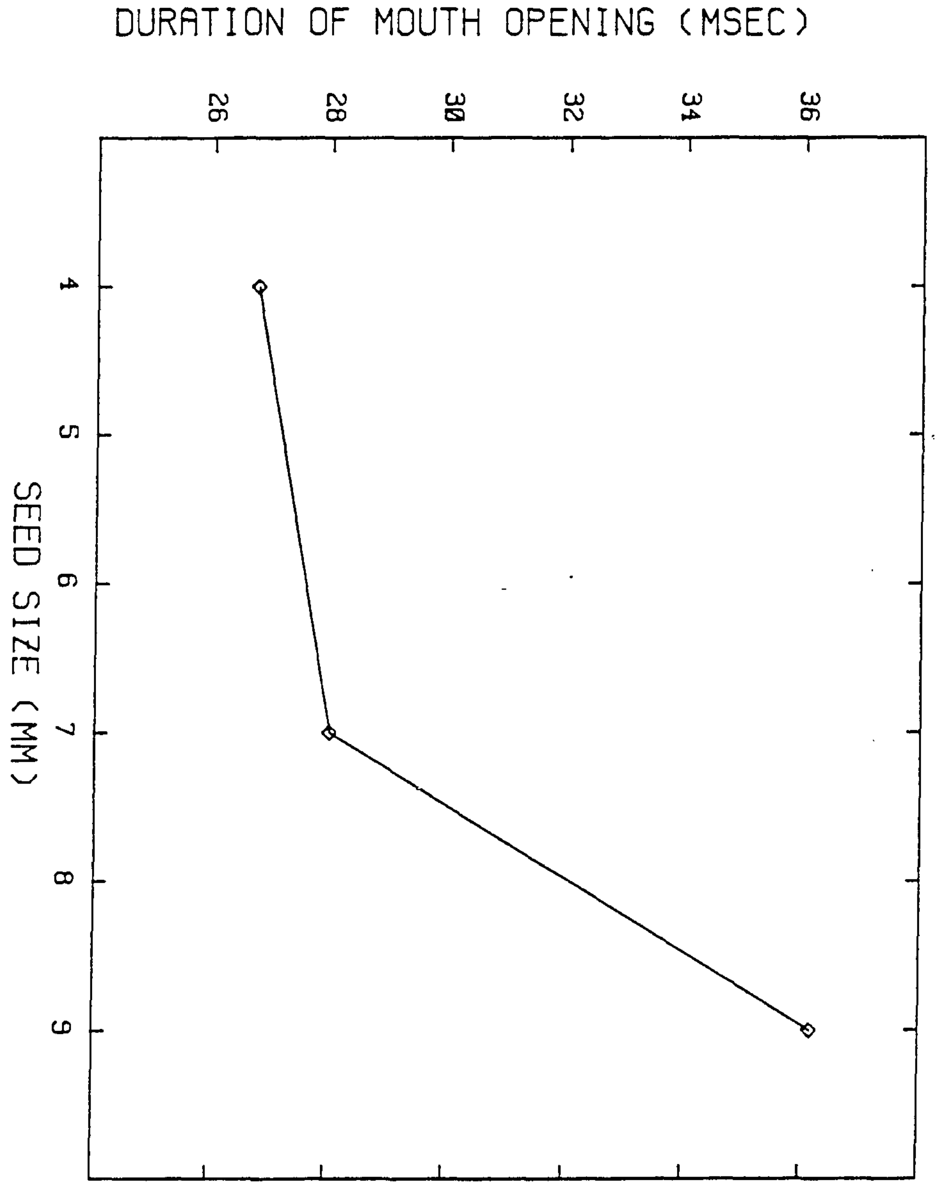

DURATION OF MOUTH OPENING (MSEC)
26
28
30
32
34
36
SEED SIZE (MM)
4
5
6
7
8
9

Figure 17. Velocity of head descent as a function of seed size for each of the 5 birds.

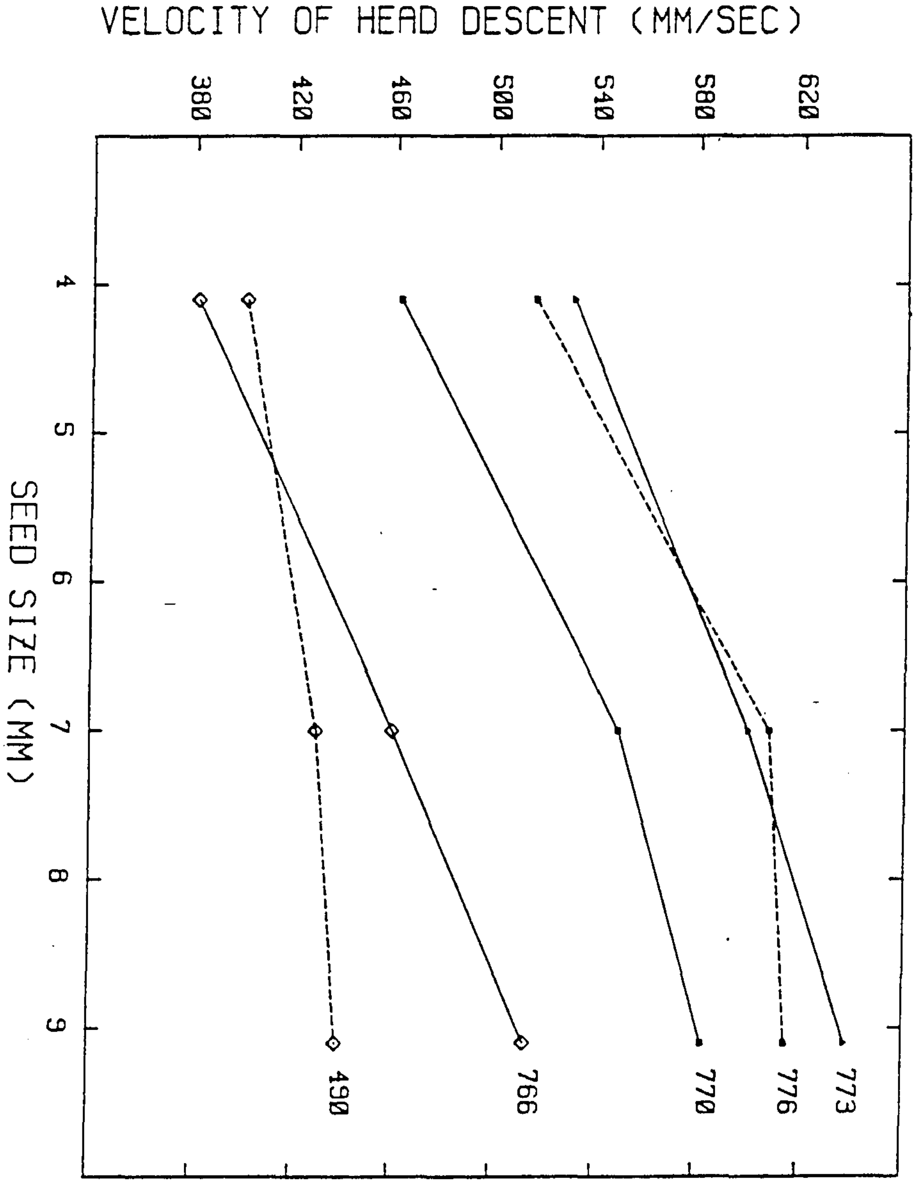

VELOCITY OF HEAD DESCENT (MM/SEC)
380
420
460
500
540
580
620
SEED SIZE (MM)
4
5
6
7
8
9
490
766
770
776
773

Figure 18. Velocity of head descent as a function of seed size across all birds.

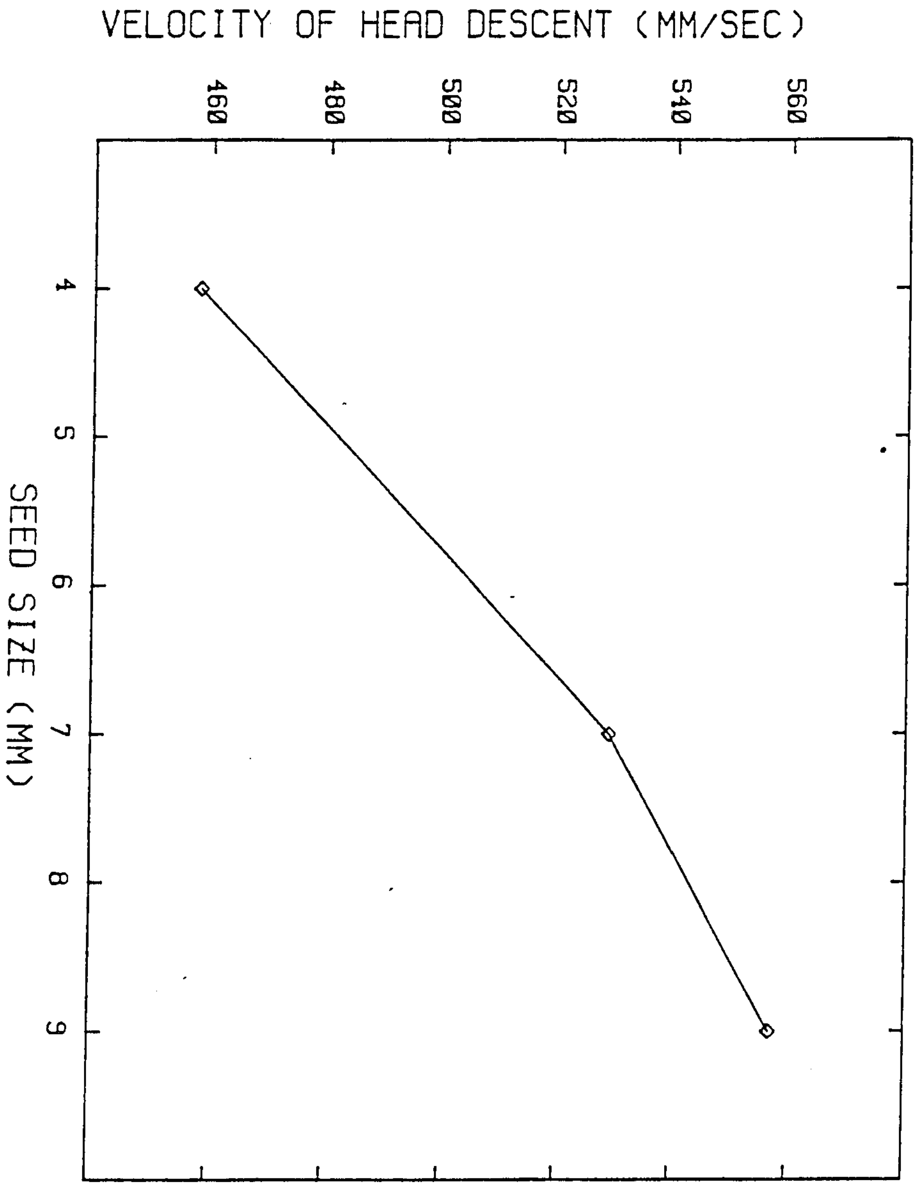

VELOCITY OF HEAD DESCENT (MM/SEC)
460
480
500
520
540
560
SEED SIZE (MM)
4
5
6
7
8
9

Figure 19. Distance from the seed at the start of head descent as a function of seed size for each of the 5 birds.

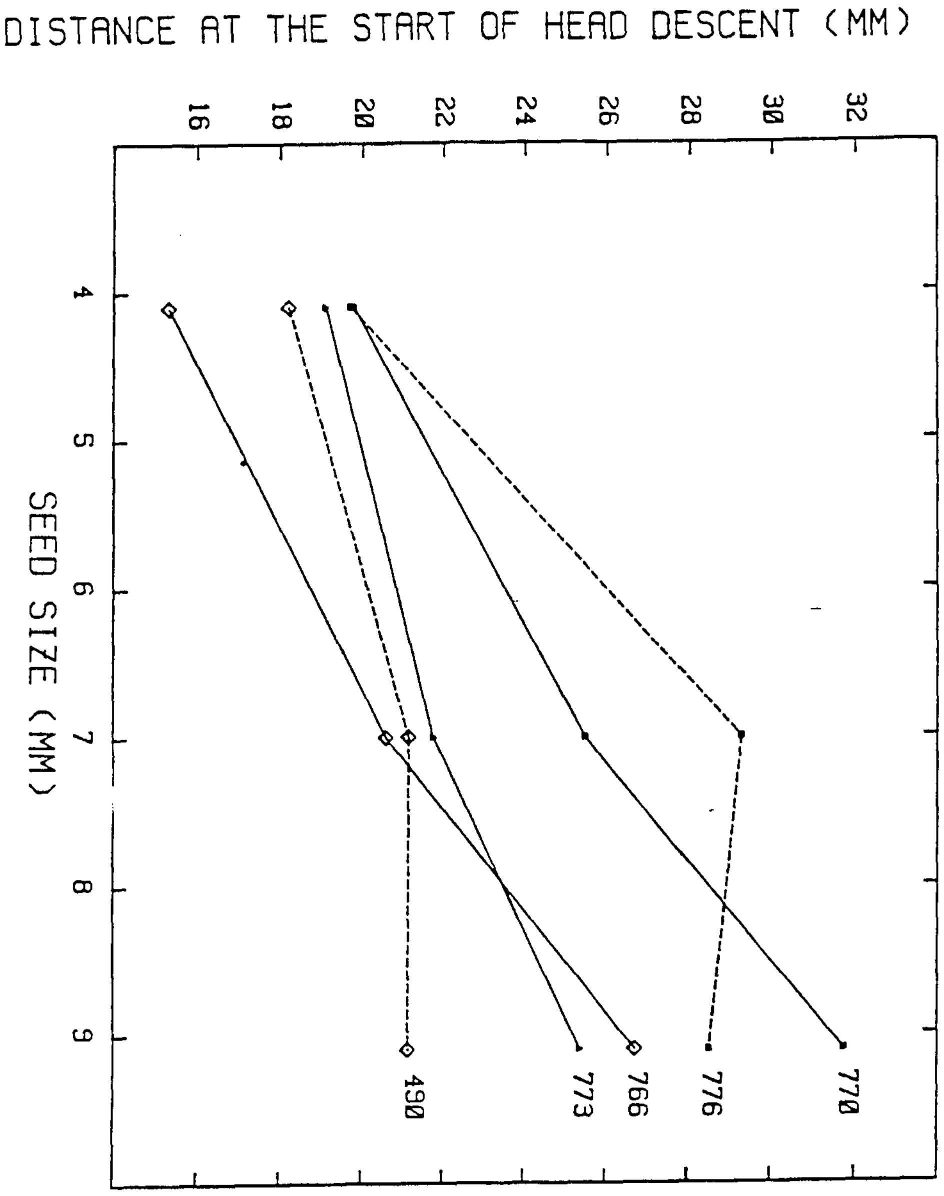

DISTANCE AT THE START OF HEAD DESCENT (MM)
16
18
20
22
24
26
28
30
32
SEED SIZE (MM)
4
5
6
7
8
9
770
776
766
773
490

Figure 20. Distance above the seed at the start of head descent as a function of seed size across all birds.

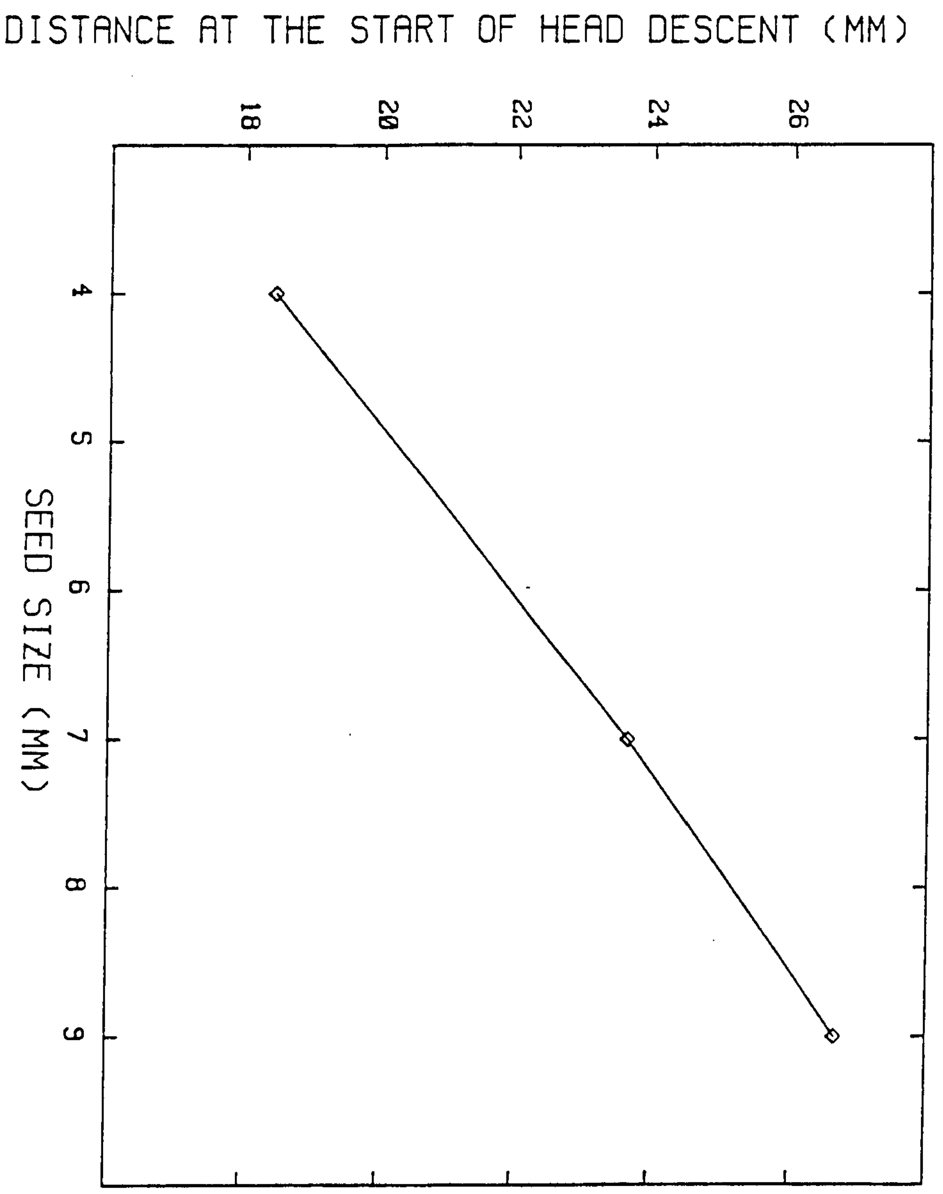

DISTANCE AT THE START OF HEAD DESCENT (MM)
18
20
22
24
26
SEED SIZE (MM)
4
5
6
7
8
9

Figure 21. Latency of mouth opening as a function of seed size for each of the 5 birds.

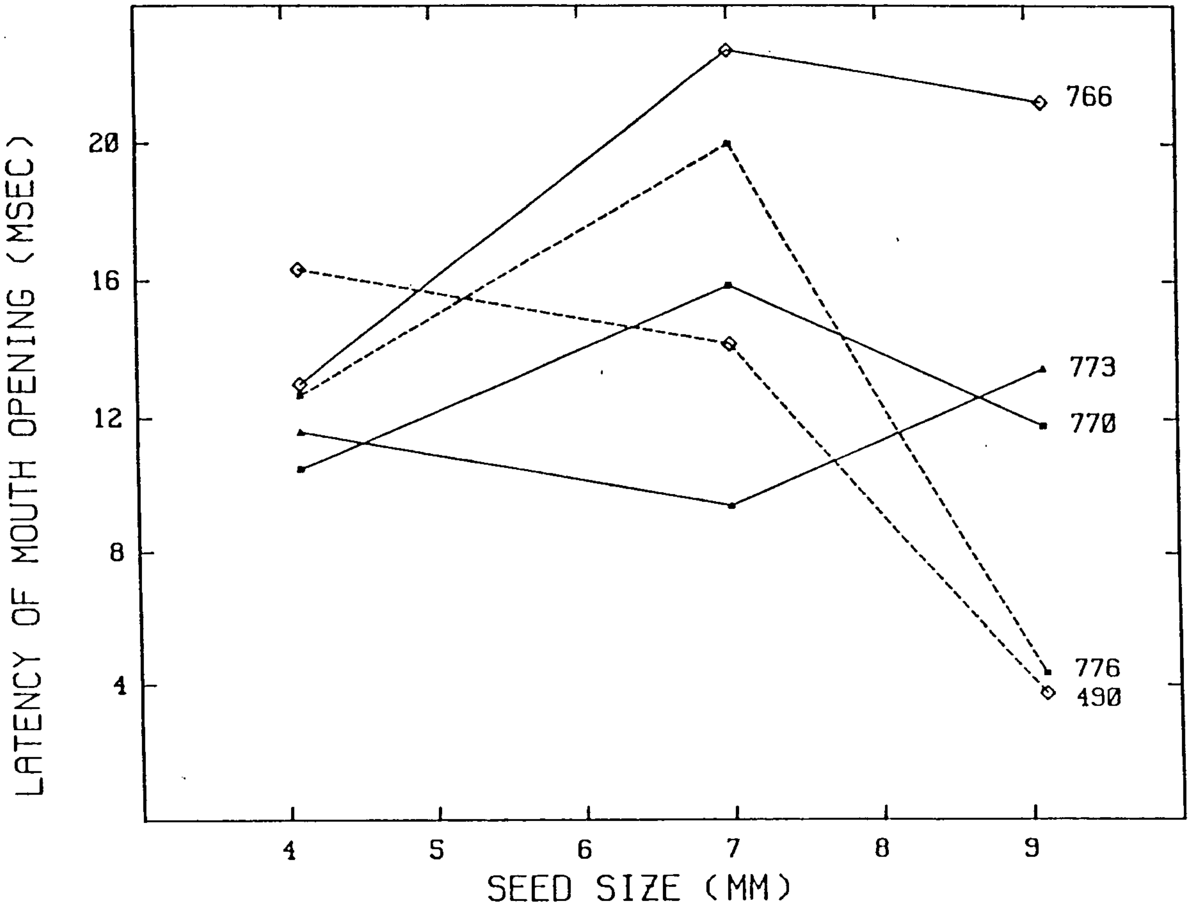
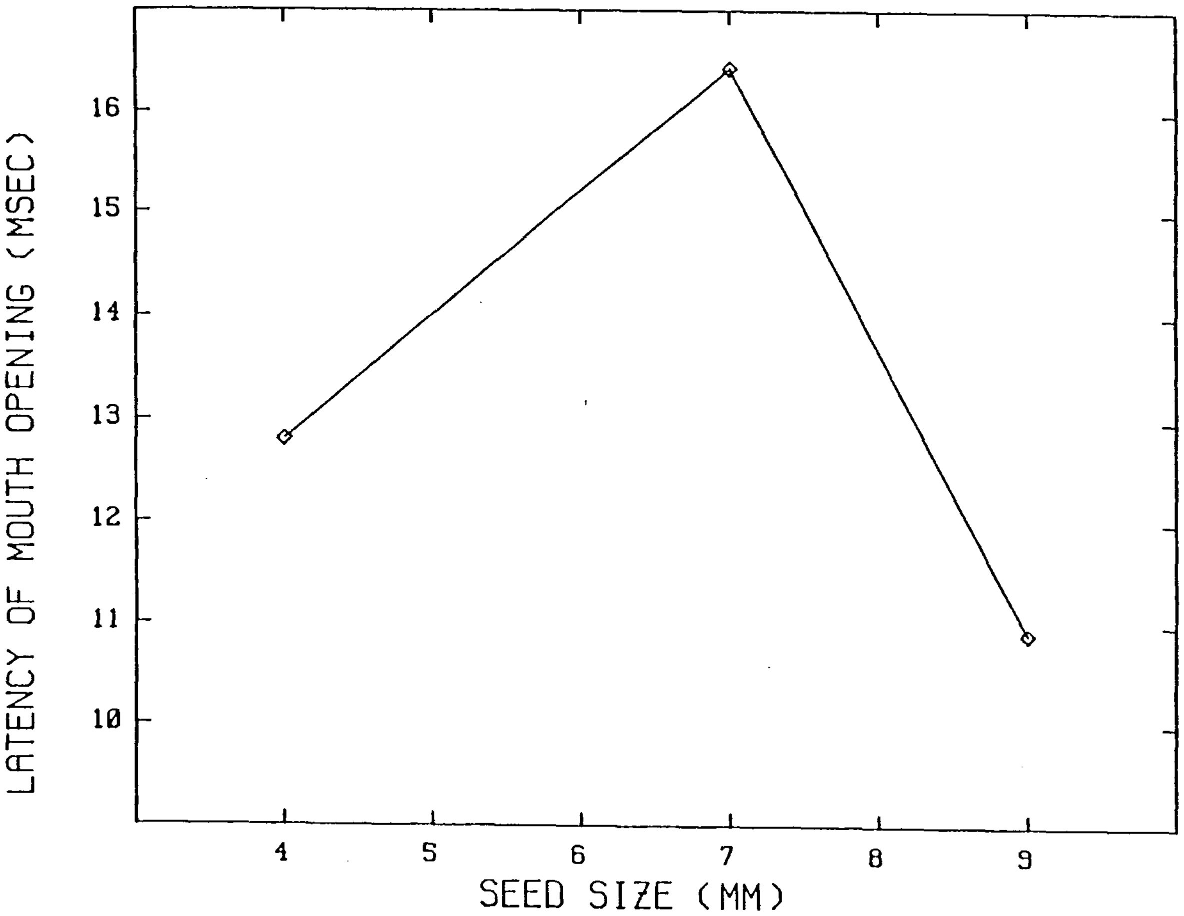

766
773
770
776
490
20
16
12
8
4
LATENCY OF MOUTH OPENING (MSEC)
4
5
6
7
8
9
SEED SIZE (MM)

Figure 22. Latency of mouth opening as a function of seed size across all birds.


LATENCY OF MOUTH OPENING (MSEC)
16
15
14
13
12
11
10
4
5
6
7
8
9
SEED SIZE (MM)

of variance (ANOVA) with repeated measures was performed on the data for each of the above factors. For each factor, Table 4 presents the means and standard deviations (across the 5 birds) for each seed size, the values of the F-statistic, the degrees of freedom and the percentage of main effect sum of squares accounted for by a linear trend. Examining the relationship of each factor with seed size indicated which factors were involved in gape adjustment.

Figures 11 through 16 present the relationship of seed size with 1) gape, 2) the velocity of mouth opening and 3) the duration of mouth opening. For both gape and velocity of mouth opening, all 5 birds show a monotonic increase with seed size. This is reflected in the shape of the mean functions for both of these factors. For the duration of mouth opening, 3 of the 5 birds show a monotonic increase with seed size. As for the remaining 2 birds, one shows an overall increase in duration as seed size increases from 4.1 mm to 9.1 mm (milo to garbonzo), however, no increase is evident from 7.0 mm to 9.1 mm (peas to garbonzo). The last bird shows an overall increase in duration as seed size increases from 4.1 mm to 9.1 mm, despite a decrease between 4.1 mm and 7.0 mm. Like the previous two factors, the mean function relating duration of mouth opening to seed size is monotonically increasing. Analysis of variance revealed

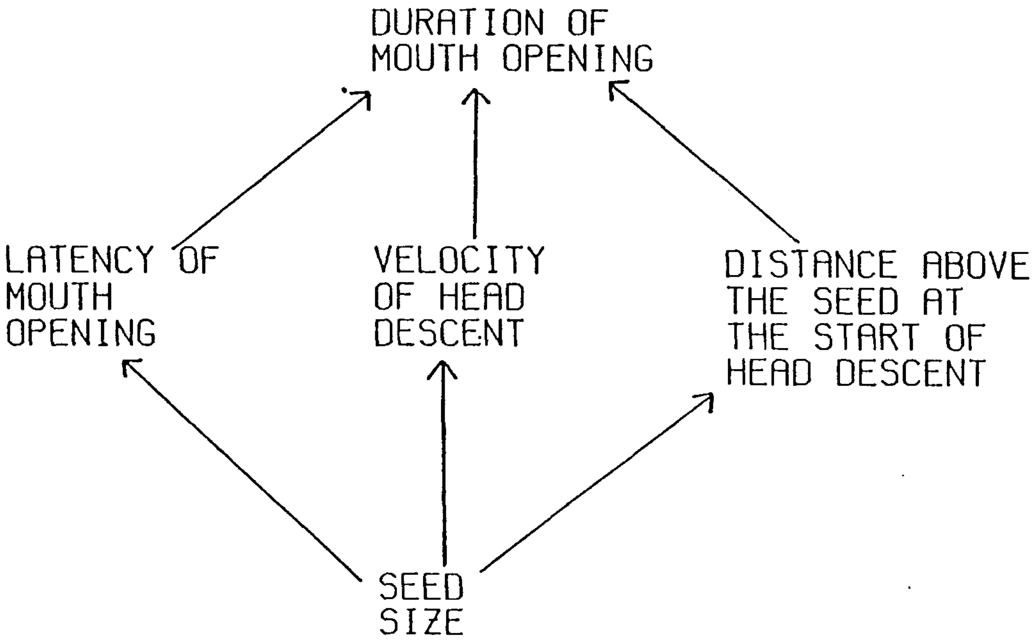
Table 4. ANOVA results for the effect of seed size on each of the factors thought to be involved in gape adjustment. VMO = velocity of mouth opening, DURMO = duration of mouth opening, VHD = velocity of head descent, DISHD = distance from the seed at the start of head descent, LMO = latency of mouth opening, * = significant (alpha = 0.05).

Factor	Seed						F(df)	% SS Linear
	Milo		Pea		Garbonzo			
	X	SD	X	SD	X	SD		
Gape (mm)	4.70	0.60	6.37	0.42	8.56	1.26	40.81(2,8)*	96.3
VMO (mm/sec)	160	10	185	16	228	33	10.19(2,8)*	100.0
DURMO (msec)	26.77	3.05	28.04	4.82	36.17	8.49	9.93(2,8)*	75.8
VHD (mm/sec)	458	67	529	81	557	82	33.43(2,8)*	98.3
DISHD (mm)	18.43	1.85	23.67	3.68	26.67	3.90	15.81(2,8)*	99.8
LMO (msec)	12.81	2.20	16.43	5.16	10.91	7.18	1.48(2,8)	5.2

a significant effect of seed size upon all three factors (gape, velocity of mouth opening and duration of mouth opening) (see Table 4). Since all mean functions were monotonically increasing, no post-hoc tests were conducted. It therefore appears that changes in both the velocity and duration of mouth opening are involved in the adjustment of gape to seed size.

Since changes in the duration of mouth opening could be mediated through changes in 1) the velocity of head descent, 2) the distance from the seed at the start of head descent or 3) the latency of mouth opening (see Figure 23), the effect of seed size on each of these factors was also investigated. Figures 17 through 22 present the relationship between seed size and each of the above factors. For the velocity of head descent, all 5 birds show a monotonic increase with increasing seed size. This is reflected in the shape of the mean function. Distance at the start of head descent increased in a monotonic fashion for 3 of the 5 birds. The remaining 2 birds show an overall increase in distance as seed size increases from 4.1 mm to 9.1 mm, however, no increase is evident from 7.0 mm to 9.1 mm. The mean function shows a monotonic increase with seed size. For latency of mouth opening, no systematic change was evident over seed size among the 5 birds, however, the mean function showed a curvilinear trend. Analysis

Figure 23. Behavioral pathways through which seed size could influence the duration of mouth opening.

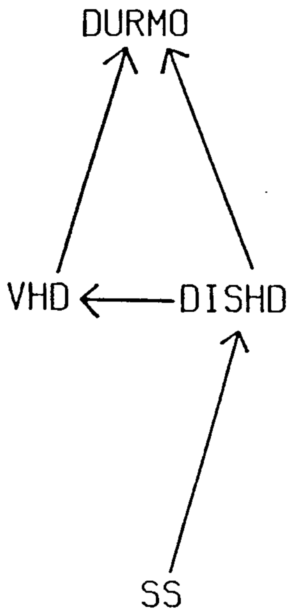

DURATION OF MOUTH OPENING
LATENCY OF MOUTH OPENING
VELOCITY OF HEAD DESCENT
DISTANCE ABOVE THE SEED AT THE START OF HEAD DESCENT
SEED SIZE

of variance revealed a significant effect of seed size upon both velocity of head descent and distance above the seed at the start of head descent. No significant effect was found upon latency (see Table 4). Therefore, both the velocity of head descent and the distance above the seed at the start of head descent appear to be mediating the effect of seed size upon the duration of mouth opening.

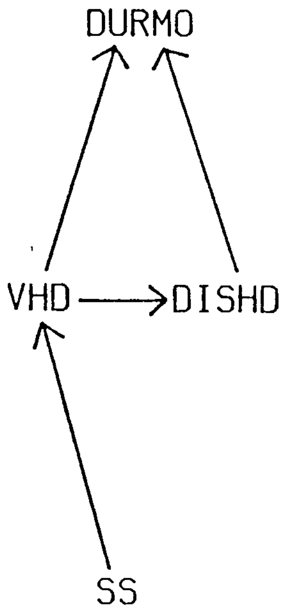
Since seed size was found to effect both the velocity of head descent and the distance above the seed at the start of head descent, the method of partial correlation was used to examine the relationship between the two factors (velocity and distance), irrespective of the effects of seed size. Partial correlations were performed on values from each opening-grasping sequence, from all 5 birds. However, since seed size measurements were not made for each sequence, mean size values (4.1 mm - milo, 7.0 mm - peas, 9.1 mm - garbonzo) were assigned to sequences involving the respective seed types. A significant correlation was found between distance above the seed at the start of head descent and velocity of head descent when controlling for the effect of seed size ($r(233) = 0.77$, $p < 0.001$).

The correlation between the velocity of head descent and the distance above the seed at the start of head descent suggested 3 possible interactions between these factors and seed size (see Figure 24): 1) seed size determines distance above the seed, which in turn determines the velocity of head descent, 2) seed size determines velocity of head descent, which in turn determines distance above the seed or 3) seed size determines both factors, which in turn influence each other. To decide between these possibilities, partial correlations were computed between seed size and each of these factors (velocity and distance), controlling for the other factor. A significant correlation was found between seed size and distance above the seed at the start of head descent when controlling for velocity of head descent ($r(233) = 0.26$, $p < 0.001$). No significant correlation was found between seed size and velocity of head descent when controlling for distance above the seed at the start of head descent ($r(233) = 0.05$). It therefore appears that Figure 24A best represents this interaction: seed size determines distance above the seed, which in turn determines the velocity of head descent. In addition, as would be expected, a significant negative correlation was found between velocity of head descent and duration of mouth opening controlling for seed size and distance above the seed ($r(232) = -0.40$, $p < 0.001$), while a significant positive correlation was found between distance above the seed and duration of mouth opening controlling for seed size and

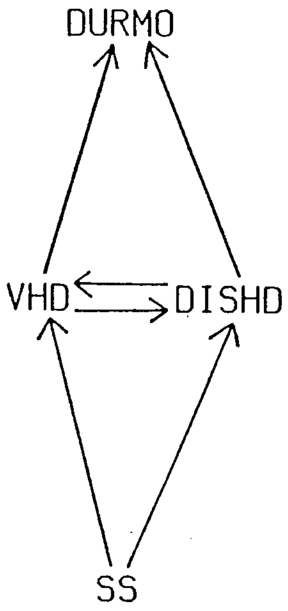
Figure 24. Possible interactions between velocity of head descent, distance above the seed at the start of head descent and seed size in determining the duration of mouth opening. SS = seed size, VHD = velocity of head descent, DISHD = distance above the seed at the start of head descent, DURMO = duration of mouth opening.


DURMO
VHD
DISHD
SS

Ⓐ


DURMO
VHD
DISHD
SS

Ⓑ


DURMO
VHD
DISHD
SS

Ⓒ

velocity of head descent ($r(232) = 0.37$, $p < 0.001$). Figure 24A therefore represents a reasonable scheme for the effect of seed size on the duration of mouth opening.

As noted above, seed size determines the distance above the seed at the start of head descent, which in turn determines the velocity of head descent. To obtain an idea of how a greater velocity of head descent is produced, the spatiotemporal organization of head descent was examined. Figure 25 presents the change in head position as a function of time from the start of head descent for 5 randomly selected eating sequences from a single bird (#770) consuming milo. The mean distance above the seed from which these sequences began was 16.6 mm. Figure 26 presents similar data for garbonzo, where the mean distance above the seed was 37.5 mm. Figures 27 and 28 respectively correspond with Figures 25 and 26 and present the change in head velocity as a function of time from the start of head descent for the same eating sequences. In comparing Figures 27 and 28, acceleration appears to be similar over the first 15-20 msec (average acceleration = 28 m/sec^2 and 30 m/sec^2, respectively), however, for milo, acceleration begins to approach zero after this point while acceleration continues for garbonzo, reaching a higher peak velocity. (Peak velocity was significantly correlated with average velocity, $r(234) = 0.95$, $p < 0.001$). It therefore

Figure 25. Head position as a function of time from the start of head descent for 5 randomly selected eating sequences from a single bird (#770) consuming milo. A positive change in position reflects movement of the head towards the seed.

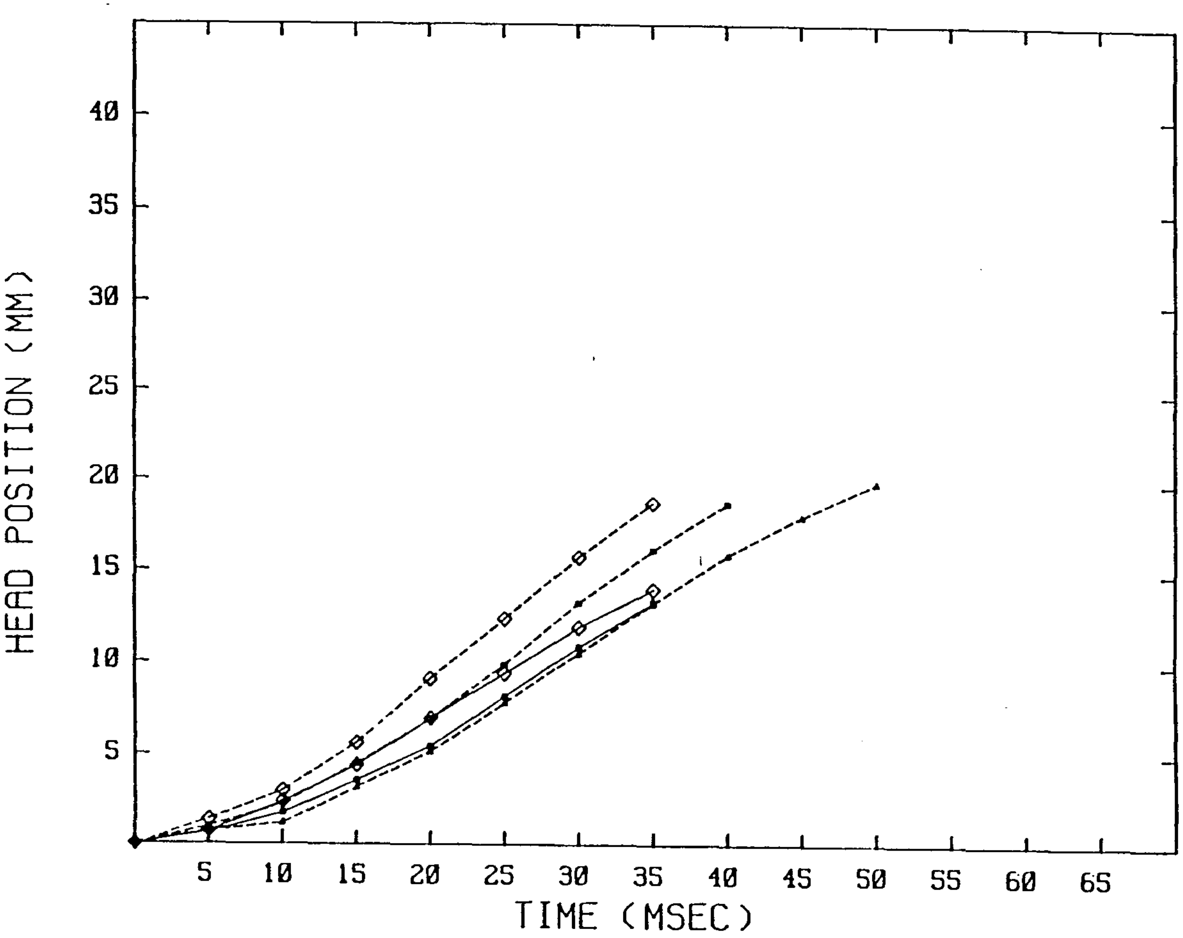

HEAD POSITION (MM)
40
35
30
25
20
15
10
5
5
10
15
20
25
30
35
40
45
50
55
60
65
TIME (MSEC)

Figure 26. Head position as a function of time from the start of head descent for 5 randomly selected eating sequences from a single bird (#770) consuming garbonzo. A positive change in position reflects movement of the head toward the seed.

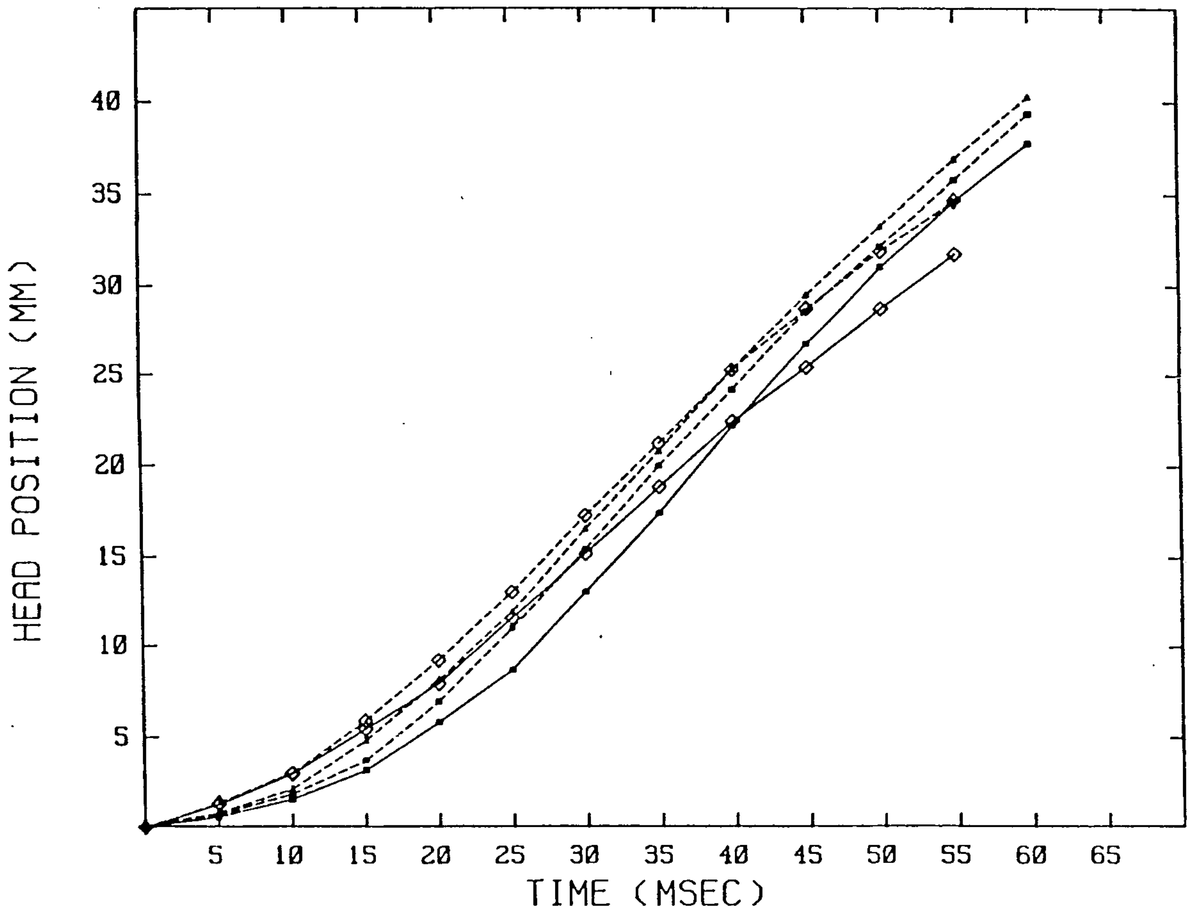

HEAD POSITION (MM)
40
35
30
25
20
15
10
5
5
10
15
20
25
30
35
40
45
50
55
60
65
TIME (MSEC)

Figure 27. Head velocity as a function of time from the start of head descent for the same 5 eating sequences presented in Figure 25.

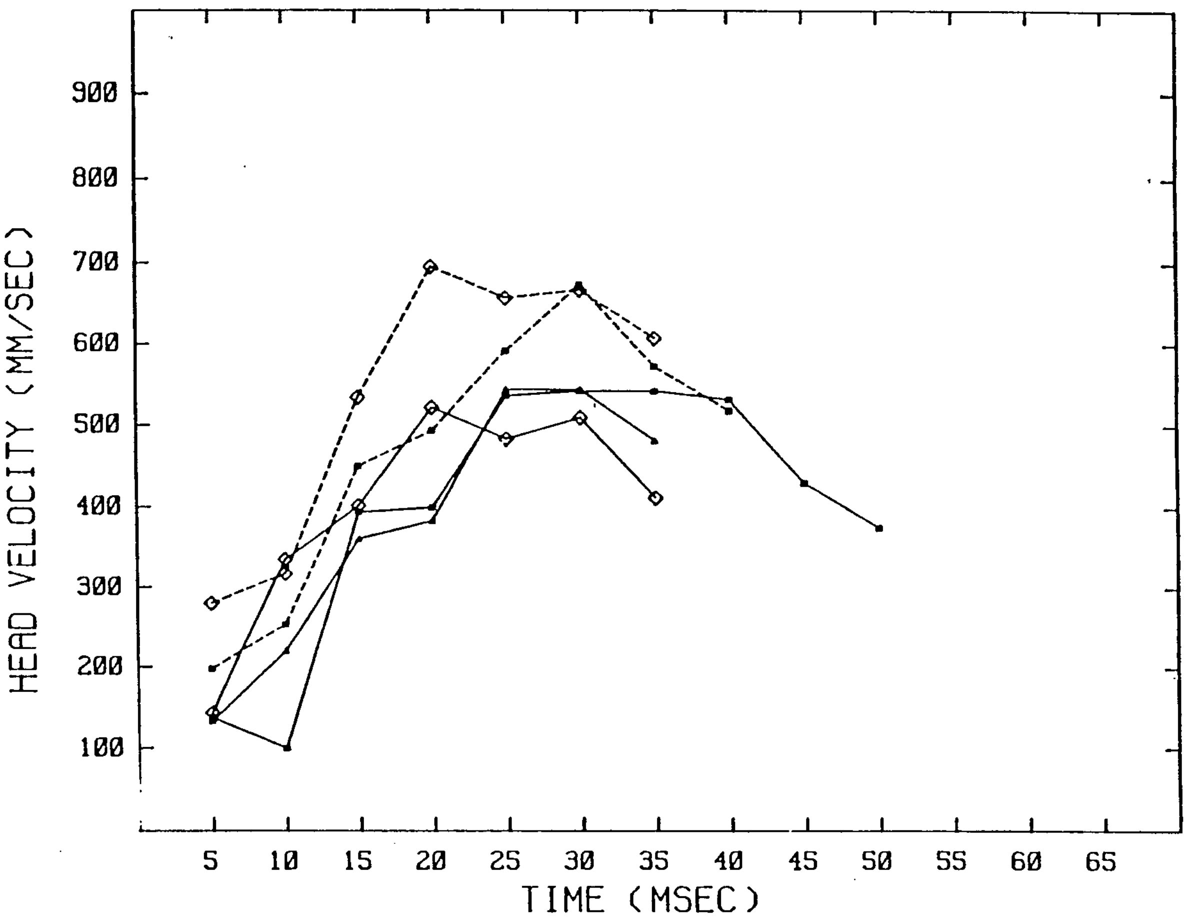
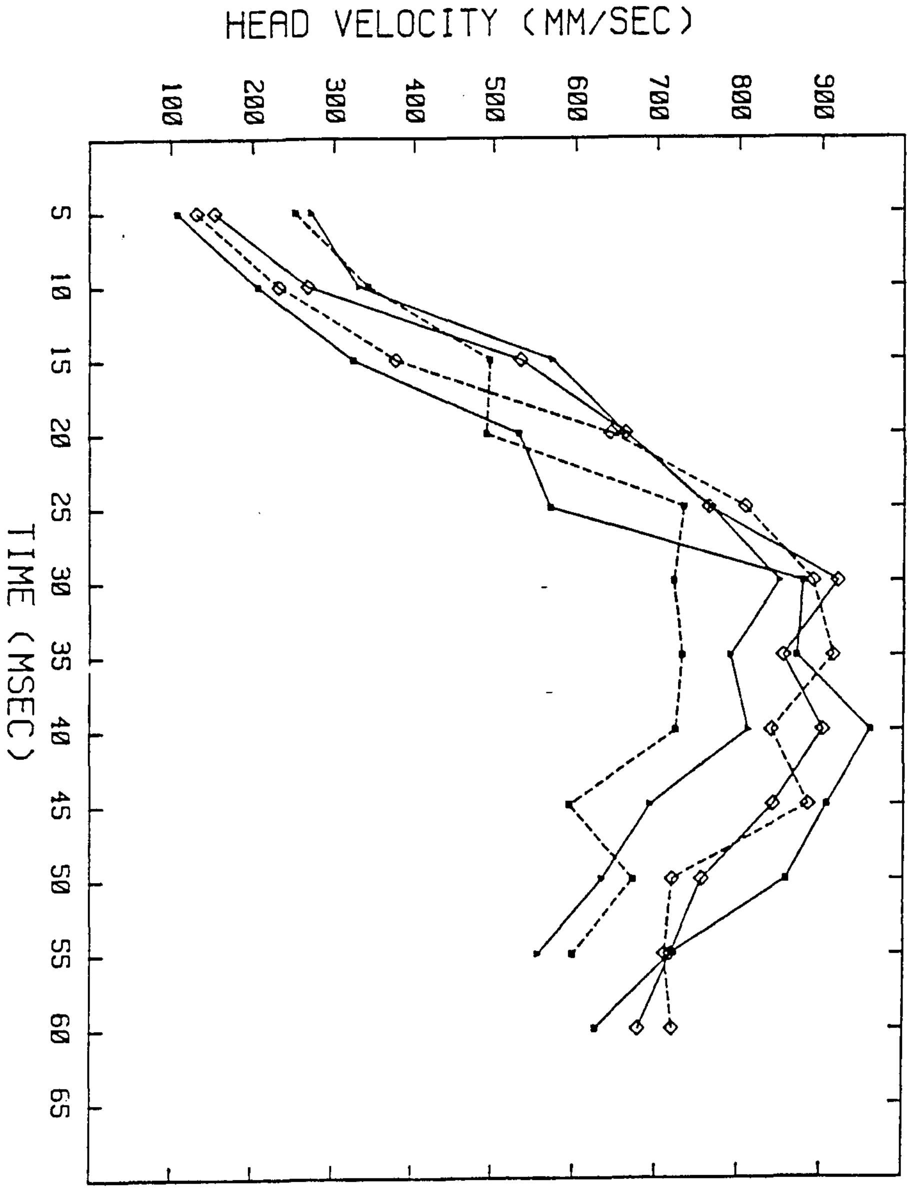

HEAD VELOCITY (MM/SEC)
900
800
700
600
500
400
300
200
100
5
10
15
20
25
30
35
40
45
50
55
60
65
TIME (MSEC)

Figure 28. Velocity of head descent as a function of time from the start of head descent for the same 5 eating sequences from Figure 26.


HEAD VELOCITY (MM/SEC)
100
200
300
400
500
600
700
800
900
TIME (MSEC)
5
10
15
20
25
30
35
40
45
50
55
60
65

appears that the greater the distance above the seed at the start of head descent, the longer the period of acceleration of the head.

The possibility that distance above the seed at the start of head descent is also related to velocity of mouth opening was investigated as well. No significant correlation was found between distance above the seed and velocity of mouth opening when seed size was controlled for ($r(233) = -0.04$). However, there was a significant correlation between seed size and velocity of mouth opening when distance above the seed was controlled for ($r(233) = 0.46$, $p < 0.001$). This suggests that the velocity of mouth opening is related to seed size rather than to the distance above the seed at the start of head descent. It also suggests that the velocity of mouth opening and the velocity of head descent are controlled by different mechanisms.

Discussion

To briefly summarize the findings of Experiment 1, both jaws were found to open during grasping for all three seed sizes, with opening of the maxilla preceding opening of the mandible by about 9 msec. The amount of opening of the 2 jaws was not different, however, it was found to vary with seed size.

In examining the basis for gape adjustments to seed size, both the velocity and duration of mouth opening were found to increase with increasing seed size. Of the 3 possible factors which could mediate the effect of seed size on duration of mouth opening (latency of mouth opening, velocity of head descent and distance above the seed at the start of head descent), only velocity of mouth opening and distance above the seed at the start of mouth opening were found to increase with increasing seed size. An analysis of partial correlations supported a model in which seed size effects the distance above the seed at the start of head descent, which in turn determines the velocity of head descent. These factors then both act to determine the duration of mouth opening.

Jaw Movements

The analysis of jaw movements suggests that

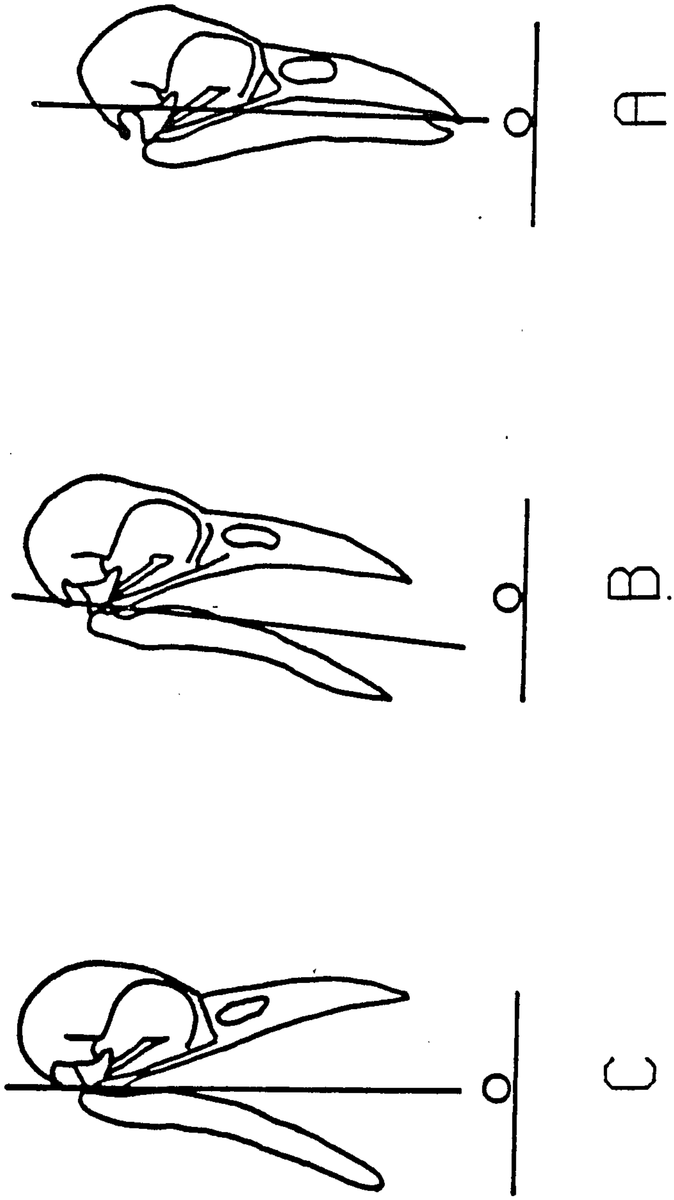
M. depressor mandibulae may not be playing a role in raising the upper jaw during the opening phase of seed grasping. This is based upon the observation that although both jaws open during grasping, protraction of the maxilla precedes mandibular depression. This suggests that the quadrate may be swinging forward before the post-orbital ligament can become loaded and hence, the depressor mandibulae muscle does not aid in maxillary protraction.

It should be stressed that the above conclusion is based solely upon an analysis of structural movement (eg. the jaws). Therefore, comments regarding internal events (eg. quadrate movement) are quite tentative. The relationship between M. depressor mandibulae and maxillary protraction could be further clarified by measurements such as the contraction sequence of the opener muscles, and stress on the post-orbital ligament during opening.

Keeping this warning in mind, the analysis also suggests that opening-grasping may be under the control of both jaw opener muscles. If M. depressor mandibulae does not aid in raising the maxilla, M. protractor quadrati is likely to be responsible for this movement. This raises the question of why two muscles would be necessary for opening-grasping when the mechanical arrangement of the pigeon skull might allow both jaws to be opened by M. depressor mandibulae alone. A possibility is that control of the maxilla by M. protractor quadrati can produce a greater excursion of this jaw than is possible through contraction of M. depressor mandibulae alone. This view is supported by the experiments of Zusi (1967), who directly stimulated the depressor mandibulae muscle of domestic chickens (Gallus domesticus) (similar in cranial morphology to the pigeon) and examined the resulting maxillary protraction. In the 4 chickens tested, maxillary displacement was only about 25% of that of mandibular displacement, during stimulation of M. depressor mandibulae. On the other hand, the present experiment demonstrated that in the pigeon, the amount of excursion of the maxilla was not significantly different from that of the mandible, when the maxilla was presumed to be under the control of M. protractor quadrati. Therefore, M. protractor quadrati may have produced more displacement of the maxilla, per unit displacement of the mandible, than M. depressor mandibulae alone.

Keeping the amount of maxillary protraction similar to that of mandibular depression permits the maintenance of a stationary axis for the beak as the jaws open (Bock, 1964). As illustrated in Figure 29, if excursion of the mandible were to be greater than that of the maxilla, this axis would be shifted. A reorientation of the head

Figure 29. Inter-beak axis with respect to the seed prior to mouth opening (A), with the mandible opening a greater amount than the maxilla (B), and with the maxilla and mandible opening similar amounts (C) (drawn from Bock, 1964).


A
B
C

would then be necessary, during the response, in order to obtain the seed. Such an adjustment would be quite difficult due to the extremely rapid nature of the pigeon's eating response. However, when maxillary protraction is comparable to mandibular depression, the axis is not shifted and no reorientation of the head is necessary.

Although the mandible may not assist in raising the upper jaw during seed grasping, it may do so in other behaviors involving jaw movements. For example, Zusi (1967) has suggested that the depressor mandibulae muscle alone may be opening both jaws when small, less powerful gapes are required. Such a mode of jaw opening might operate during behaviors such as preening. Bock (1964) has proposed a similar mode involving both jaw opener muscles when large, forceful gaping is necessary. This mechanism might be utilized in behaviors such as nest construction or maintenance. A wide diversity of jaw movement mechanisms would be advantageous to the pigeon, since the beak is its major means of manipulating the environment. Whether such diversity exists can only be verified by studying jaw movements in a wide range of behavioral situations. The existence of multiple jaw movement mechanisms would imply an equally diverse system of neural networks imposed upon the jaw motor nuclei.

Gape Adjustment

As noted above, both the velocity and the duration of mouth opening increase with increasing seed size. This raises the question of why more than one characteristic of the eating response changes to generate the appropriate gape. A possible explanation is that the amount of change possible in a single factor may not be able to produce the amount of gape required. For example, velocity of mouth opening may have a limited range over which it can physically vary. This range may not be able to produce a range of gapes useful to the organism in dealing with its environment. Adding variation of an additional factor, such as duration of mouth opening, might provide a more functional range of gape values.

In an analysis of visually guided pecking in the pigeon, Goodale (1982) has observed 2 periods of head fixation during eating. The secondary fixation point (F2) is that which immediately precedes the ballistic portion of the response. The height of the head at F2 is equivalent to the distance from the seed at the start of head descent in the present experiment. The initial fixation point (F1) (not examined in the present experiment) occurs about 40 mm above F2. According to Goodale, at the initial fixation point, the decision to peck at the seed is made, whereas at the secondary fixation point, information regarding the depth, size and location of the object is calculated. The results of the present experiment indicate that at least some size information is being processed at the initial fixation point, since the height of the head at the secondary point changes with seed size. The view that the height of the secondary fixation point is determined at the initial point is supported by the findings of Zweers (1982) that the head never reverses direction following the initial fixation point. Perhaps one way to test this hypothesis would be to change the apparent size, position or depth of the target between F1 and F2, and determine the effect upon pecking efficiency. It would also be interesting to determine whether the height of the initial fixation point varies as a function of seed size. If the initial fixation point always occurred at the same height, it would be a more reasonable location for judging the differential size of objects than the secondary fixation point since retinal image size would only be effected by the object size. At F2, judgements of the differential size of objects are complicated by the variations in distance from the seed.

As noted above, the velocity of head descent is determined by the distance above the seed at the start of head descent. This relationship appears to result from longer periods of head acceleration associated with those reponses which begin farther from the seed. A similar relationship exists in the occulomotor system between peak velocity (and average velocity) and saccadic amplitude. This is referred to as the "main sequence" for normal saccades (Bahill, Clark and Stark, 1975). It has been suggested that this relationship derives from variations in the width of a controller pulse. This signal can be represented by the burst of activity which preceed saccadic eye movements (see Fuchs and Luschei, 1970). Presumably, the muscles are applying accelerating forces to the eyeball during the controller pulse. Therefore, longer pulses allow a greater peak velocity of eye movement to be reached. Given the data presented in Figures 27 and 28, a similar mechanism may underly the attainment of greater velocity during head descent. That is, longer controller pulses may be produced if the head is farther from the seed, and hence, greater velocities are attained.

Since seed size was found to determine both the velocity of mouth opening and the distance above the seed at the start of head descent, it appears that at least two different efferent systems are involved in the adjustment of gape to seed size. Both neck motoneurons, as well as jaw motoneurons, probably receive afferent input which varies with seed size. An analysis of the neural substrate of gape adjustment to seed size should therefore concentrate on the neural control of both neck and jaw systems. Wild and Zeigler (1980) and Berkhoudt, Klein and Zeigler (1982) have respectively identified the motor innervation of the pigeon's jaw muscles and the afferents to these motoneurons. A similar analysis would be in order for the neck muscles.

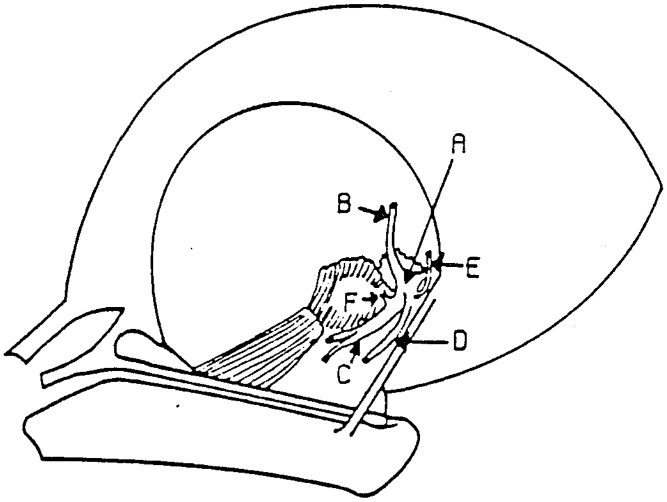
Experiment 2- Final common path for opening-grasping.

In Experiment 1, an analysis of the topography and spatiotemporal organization of opening-grasping was presented. In Experiment 2, the primary efferent control of this behavior will be examined.

Using dissection in conjunction with the horseradish peroxidase (HRP) technique, Wild and Zeigler (1980) identified the brainstem motoneurons innervating the pigeon's jaw opener muscles. M. protractor quadrati is innervated by a single nerve branch (see Figure 30). The cells of origin for this nerve (see Figure 31) are located within the ipsilateral main trigeminal motor nucleus, comprising a dorsomedial subnucleus. M. depressor mandibulae is innervated by 3 branches of the facial motor nerve (see Figure 30) which originates in the dorsal facial nucleus (see Figure 31).

Since the arrangement of the pigeon's jaw apparatus is characteristic of coupled kinesis, the depressor mandibulae muscle alone might be able to open both jaws. Therefore, the final common path for opening-grasping might be comprised of cells of the dorsal facial nucleus alone. However, the results of Experiment 1 suggest that both M. protractor quadrati and M. depressor mandibulae may be producing the observed opening-grasping topography. If this is true, the final common path for

Figure 30. The trigeminal motor innervation of M. protractor quadrati (F, top) and the facial motor innervation of M. depressor mandibulae (N. depressor mandibulae, bottom) (drawn from Wild and Zeigler, 1980). A = trigeminal ganglion, B = ophthalmic division, C = mandibular division, D = descending maxillary division, E = ascending maxillary division, F = N. protractor quadrati.


A
B
E
F
D
C

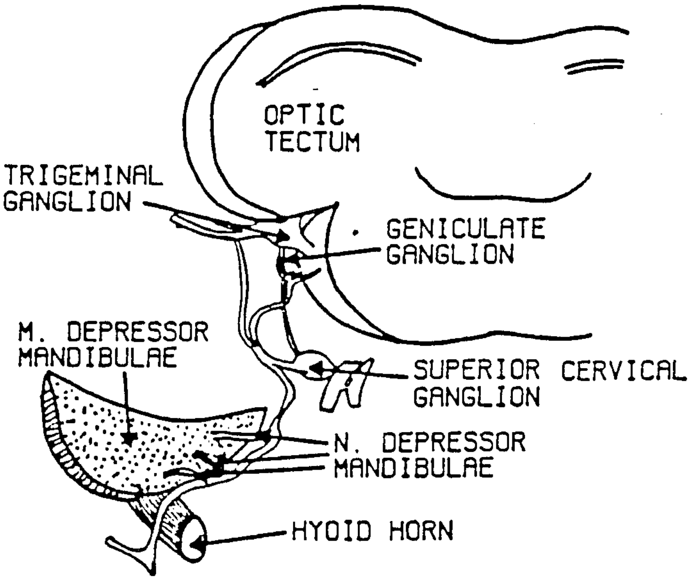
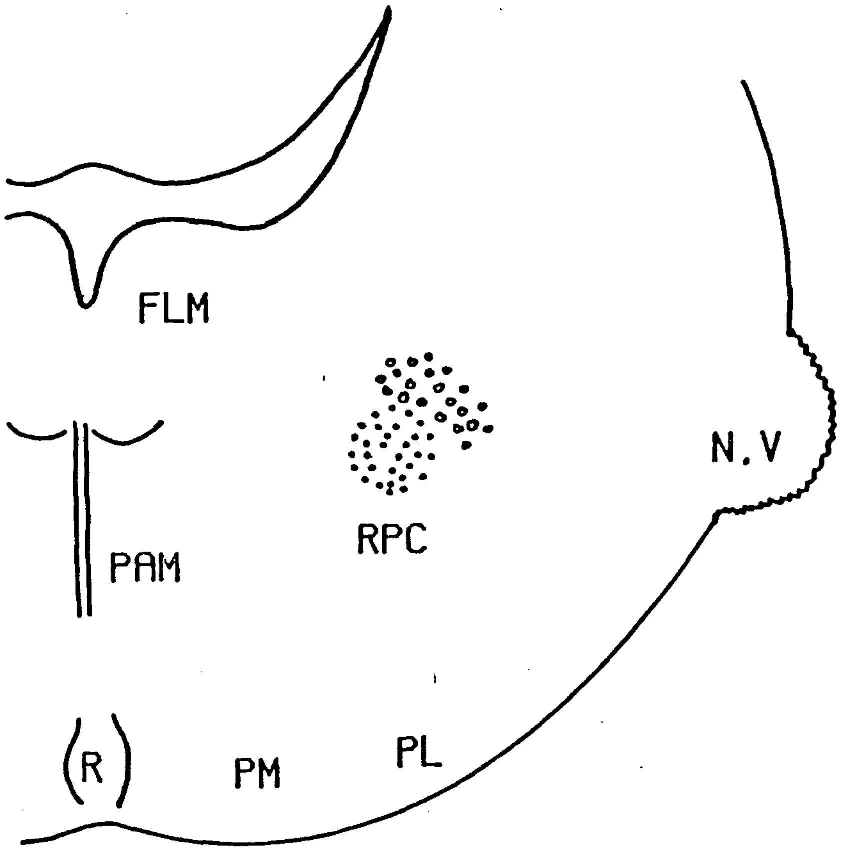

OPTIC TECTUM
TRIGEMINAL GANGLION
GENICULATE GANGLION
M. DEPRESSOR MANDIBULAE
SUPERIOR CERVICAL GANGLION
N. DEPRESSOR MANDIBULAE
HYOID HORN

Figure 31. Brainstem location of retrogradely labelled cell bodies representing the jaw opener muscles (drawn from Wild and Zeigler, 1980). Open circles = M. protractor quadrati, solid circles = M. depressor mandibulae.



A 0.9-0.7

opening-grasping should be composed of neurons of the main trigeminal motor nucleus, as well as those of the dorsal facial nucleus. To test this, the nerves innervating the pigeon's jaw opener muscles will be sequentially sectioned and the influence upon individual jaw movements will be assessed. If the protractor quadrati muscle is involved in opening-grasping and hence the trigeminal motor nucleus is part of the final common path for this behavior, then sectioning the facial innervation of M. depressor mandibulae should abolish opening of the lower jaw, while the upper jaw continues to open. Subsequent section of the trigeminal innervation of M. protractor quadrati should eliminate any remaining jaw opening if the trigeminal and facial motor nuclei compose the final common path for opening-grasping.

Method

Subjects, Apparatus and Experimental Design

Three birds from Experiment 1 were randomly selected for a 2 stage denervation procedure. In Stage 1, the facial motor branches innervating M. depressor mandibulae were cut, and in Stage 2, the trigeminal motor branch to M. protractor quadrati was sectioned. Feeding films were taken after each surgical stage, with the apparatus described in Experiment 1. Two birds were used as sham controls. They received the same surgical and behavioral treatment as the denervated birds, however, no motor nerves were cut. The paradigm for Experiment 2 is presented in Table 5.

Surgical Procedures

Sectioning N. depressor mandibulae. Prior to surgery, animals were fed to 90% of ad lib weight to compensate for the witholding of food during the operation and the recovery period. Birds were anesthesized with Chlor-O-Pent and mounted in the stereotaxic apparatus ventral side up. The retroarticular process of the mandible was located by touch, and an incision was made extending 1 cm caudally. The remainder of the operation was carried out with the aid of a Zeiss dissecting microscope. Following retraction of the skin flaps, a

Table 5. Experimental design for Experiment 2.

	Experiment 2			
	Surgical (N=3)			
Normal films (Experiment 1)	Section of facial innervation of M. depressor mandibulae	Post-operative films 1	Section of trigeminal innervation of M. protractor quadrati	Post-operative films 2
	Sham (N=2)			
	Same as surgical without nerve cut	Post-operative films 1	Same as surgical without nerve cut	Post-operative films 2

hole was made in the stylohyoideus muscle, exposing the facial nerve trunk as it emerged between the ventral portion of M. depressor mandibulae (M.dm) and the hyoid horn. After retracting the hyoid horn, the facial nerve was separated from its membranous attachments to M.dm as it was followed dorsally, toward its exit from the ventral brain case. Applying tension to the nerve trunk accentuated the 3 branches innervating M.dm (see Figure 30), which were then cut sequentially beginning with the main branch. The trunk was then carefully inspected for anomalous connections to M.dm. No such connections were found in any of the animals. A small piece of Gelfoam was then inserted between the facial trunk and the muscle in order to inhibit or retard regeneration of the severed nerve branches. The wound was then closed with 6-0 silk sutures and sprinkled with Neosporin powder. The identical procedure was then performed on the contralateral side. The animal was removed from the stereotaxic apparatus and placed in the home cage to recover for 48 hours. The bilateral procedure lasted approximately 2 hours from the time of injection.

Sectioning of N. protractor quadrati. Due to the difficulty of this procedure, it was performed on 2 consecutive days, one side per day. The animal was anesthesized, its head feathers were trimmed and it was mounted in the stereotaxic apparatus in the normal fashion. An incision was made in the skin overlying the supraorbital rim and was extended in a semicircular fashion around the caudal rim of the orbit. The anterior skin flap was then reflected forward, and the periosteum overlying the exposed area was removed. The remainder of the procedure was carried out with the aid of a dissecting microscope. The dermotemporalis muscle was separated from the skull until the origin of M. adductor externus was exposed. Contact with this muscle was avoided, except for periodic moistening with a saline solution. The skull was then scraped clean and a shallow hole was drilled extending over the area previously covered by M. dermotemporalis. The matrix of bone connecting the optic tectum, the inferior lateral surface of the telencephalon and the caudal wall of the orbit was then drilled away. After removing the thin bony plate covering the tectum, the structure was carefully retracted so as not to damage the dura and underlying membranes. The trigeminal (Gasserian) ganglion could then be seen lying under the remaining tectal plate. Removing this bone exposed the maxillary and mandibular trigeminal divisions. As can be seen in Figure 30, the innervation of M. protractor quadrati (N. protractor quadrati (N.pq)) ramifies from the medial side of the mandibular division and travels through the wall of the orbit. In order to expose N.pq, small pieces of bone were picked away from the orbital wall where it meets the bony sheath of the mandibular division. Applying pressure to the mandibular division caused N.pq to stand out from the spongy tissue which surrounds it, and the nerve was cut. The area was then checked to make sure that N.pq was cleanly severed. A small piece of Gelfoam was placed over the mandibular branch at the point of the cut in order to inhibit or retard regeneration of N.pq. After removing the tectal retractor, the remainder of the cavity produced by bone removal was packed with moist Gelfoam. The wound was closed with 6-0 silk sutures and Neosporin powder was applied. The animal was removed from the apparatus and placed in the home cage to recover for 48 hours. The identical procedure was performed on the opposite side on the following day. For each side, the operation lasted approximately three and a half hours from the time of initial injection.

Behavioral Procedures

Following recovery from each of the surgical procedures, post-operative feeding films were taken. The procedure was the same as for Experiment 1, except only chick peas were used.

After filming the N. depressor mandibulae animals, they were force fed 3 times the daily ration to compensate for 1) the inability to obtain food during filming, and 2) the witholding of food during Stage 2 surgery. By placing seeds at the back of the buccal cavity, force feeding bypassed all components of the feeding response except swallowing, thereby minimizing practice effects upon feeding performance.

Data Analysis

Preliminary review and frame-by-frame analysis of feeding films were performed in the same fashion as Experiment 1.

In Experiment 1, jaw displacement was measured from the start of mouth opening through block zero (the average of frame zero and the frame prior to it). The same was true for Experiment 2, except in those cases where animals had both N. depressor mandibulae and M. protractor quadrati bilaterally sectioned. These birds did not exhibit a distinct period of mouth opening, and therefore, a new method was needed for defining the interval over which jaw displacement would be examined. The start of this interval was defined by the mean latency prior to block zero, at which mouth opening began for normal (pre-operative) birds eating garbonzos. This value was determined from 10 pre-operative eating sequences: two randomly selected from each of the 5 birds. This mean latency was 39.5 msec. Therefore, for animals with combined nerve sections (N.pq and N.dm), jaw displacement was measured starting 8 blocks (40 msec) prior to block zero.

Results

A total of 109 post-operative opening-grasping sequences (3468 frames) were analyzed. Table 6 shows the breakdown by bird and surgical condition.

Nerve section

For the nerve sectioned animals, the mean change in position of the maxilla and mandible was determined after each surgical stage. A one-tailed dependent measures t-test was performed on each of the mean differences to test whether they were equal to zero. The mean and standard deviation of the difference scores, in addition to the value of the t-statistic, is presented in Table 7 for each jaw of each bird, following section of N. depressor mandibulae. Pre-operative mean difference scores for garbonzo are also shown. For the maxilla, a positive value reflects upward movement and for the mandible, a positive value reflects downward movement. The significance level used in each test was 0.01. Since 6 tests were performed, this kept the probability of one or more type I errors at 5.9%. In all cases, the mean change in mandible position did not differ from zero, while the mean change in maxilla position was significantly greater than zero. This is reflected in Figure 32 which is an example of a single grasping

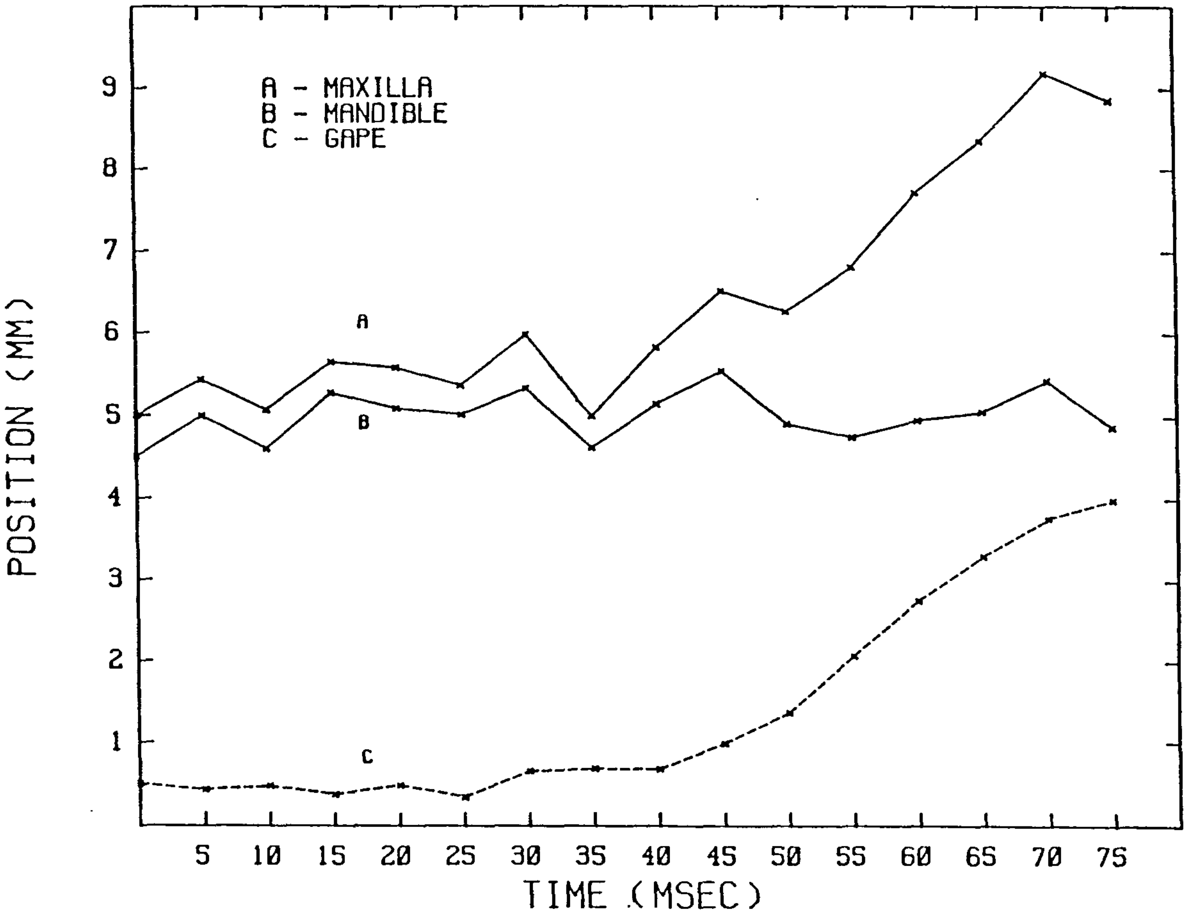
Table 6. Number of grasping sequences analyzed in Experiment 2, by bird and surgical condition.

	Surgical Condition	
	Post N. depressor mandibulae	Post N. protractor quadrati
Nerve Section		
#490	12	16
#766	12	10
#770	8	19
Sham		
#773	7	10
#776	8	7

Table 7. Mean change in position of the maxilla and mandible (in mm) following section of N.dm. The standard deviation and t statistic for these mean changes is also presented, along with pre-operative values for garbonzo. MX = maxilla, MD = mandible, * = significant (alpha = 0.01).

Bird #	Post N. Depressor Mandibulae		
	$\bar{D}$ (Pre-op)	SD	t(df)
490	MX- 2.96 (3.20)	0.90	11.39(11)*
	MD- 0.66 (6.39)	0.80	2.75(10)
766	MX- 3.93 (3.53)	1.37	9.97(11)*
	MD--0.04 (2.46)	1.07	-0.13(11)
770	MX- 3.10 (4.01)	0.71	12.44(7)*
	MD--0.62 (3.32)	0.58	-3.02(7)

Figure 32. Position of the maxilla, position of the mandible and gape over the course of a single grasping sequence following bilateral section of the depressor mandibulae nerve.


A - MAXILLA
B - MANDIBLE
C - GAPE
A
B
C
POSITION (MM)
1
2
3
4
5
6
7
8
9
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
TIME (MSEC)

sequence from an N.dm sectioned bird.

Table 8 presents the mean difference scores for the maxilla and mandible of each bird following N. protractor quadrati section. The standard deviations, t-statistics (alpha = 0.01) and pre-operative values for each mean are also presented. For all birds, neither the maxilla nor the mandible showed a mean change in position significantly different from zero. This is reflected in Figure 33, which is an example of a single grasping sequence following N.pq section.

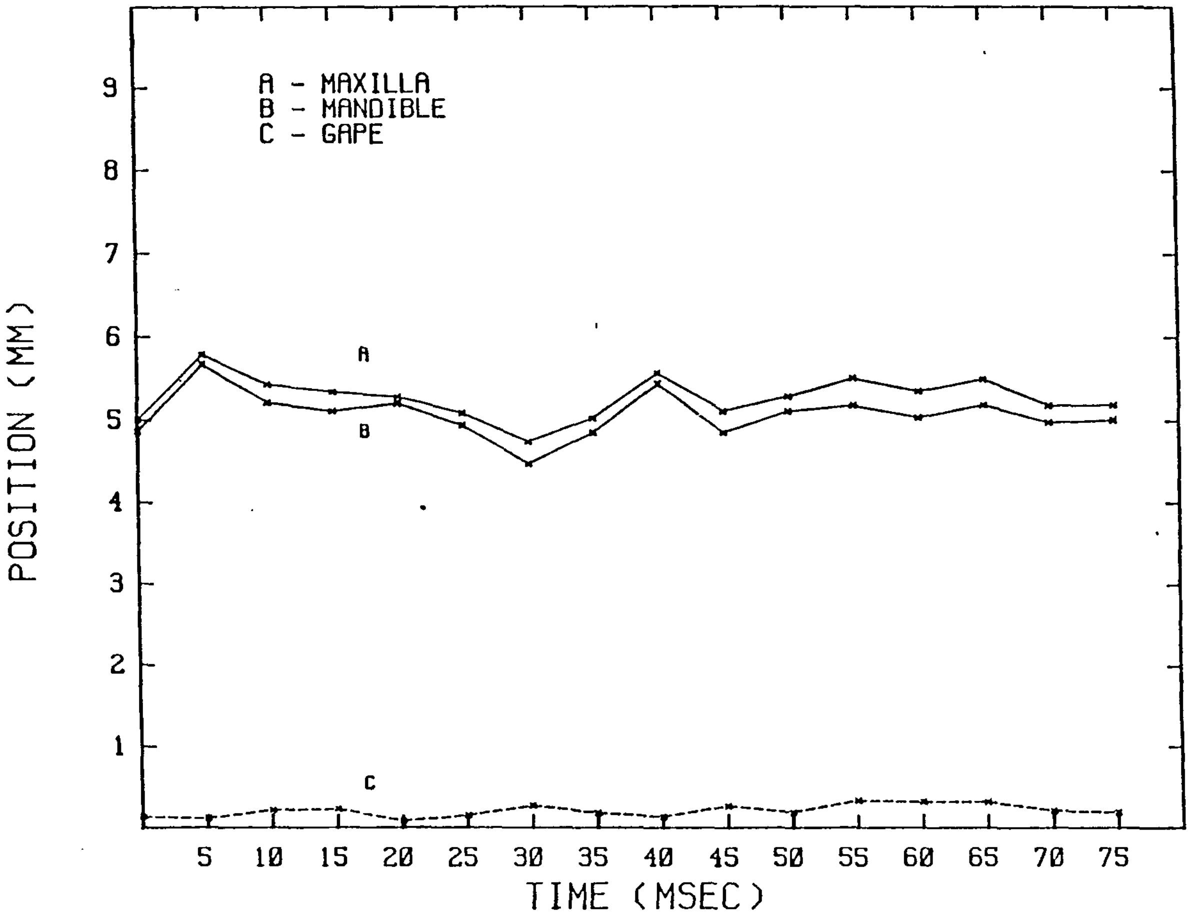
Sham surgery

Mean change scores were also determined for the maxilla and mandible of each sham animal, following each sham surgical stage. These mean values and their corresponding standard deviations are presented in Table 9, along with the pre-operative mean change values for the 2 birds. To determine whether the sham N. depressor mandibulae procedure influenced the amount of mandibular opening, a one-tailed independent groups t-test was used to compare the pre-operative change in mandible position with the change following sham N.dm surgery, for each bird. No significant difference was found between these two means for either #773 ($t(18) = 1.28$) or #776 ($t(14) = 0.78$). To examine the effect of sham N.pq surgery upon maxilla opening, the mean change in maxilla position

Table 8. Mean change in position of the maxilla and mandible (in mm) following N.pq section. The standard deviation and *t* statistic for these mean changes are also presented, along with pre-operative values for garbonzo. MX = maxilla, MD = mandible.

Bird #	Post N. Protractor Quadrati		
	$\bar{D}$ (Pre-op)	SD	t(df)
490	MX- 0.26 (3.20)	1.02	1.02(15)
	MD- 0.08 (6.39)	0.97	0.33(15)
766	MX- 0.36 (3.53)	0.72	1.59(9)
	MD--0.27 (2.46)	0.65	-1.31(9)
770	MX- 0.08 (4.01)	0.92	0.38(18)
	MD--0.06 (3.32)	1.05	-0.25(18)

Figure 33. Position of the maxilla, position of the mandible and gape over the course of a single grasping sequence after adding bilateral section of the protractor quadrati nerve to bilateral section of the depressor mandibulae nerve.


A - MAXILLA
B - MANDIBLE
C - GAPE
A
B
C
POSITION (MM)
1
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40
45
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55
60
65
70
75
TIME (MSEC)

Table 9. Mean change in position of the maxilla and mandible (in mm) pre-operatively and following each sham surgical stage. Standard deviations are also presented. MX = maxilla, MD = mandible.

Bird #		Surgical Condition		
		Pre-op	Post sham N. depressor mandibulae	Post sham N. protractor quadrati
773	MX-	3.03 ± 1.17	4.34 ± 1.29	3.15 ± 0.87
	MD-	2.52 ± 1.21	3.45 ± 2.08	3.65 ± 1.51
776	MX-	3.16 ± 1.09	3.76 ± 0.96	3.31 ± 0.68
	MD-	4.52 ± 1.21	3.98 ± 1.55	3.13 ± 0.51

following sham N.pq surgery was compared with the change following sham N.dm surgery, for both birds. Again, no significant difference was found between the 2 means for either #773 (t(15) = 2.28) or #776 (t(13) = 1.03). An alpha of 0.01 was used for each of the 4 tests to keep the probability of one or more type I errors at 4.0%.

Discussion

The maxillary protraction observed in all 3 birds following section of the depressor mandibulae nerve (N.dm) supports the inference from Experiment 1 that M. protractor quadrati is involved in opening-grasping, as well as M. depressor mandibulae. It also suggests that the protractor quadrati nerve is a component of the final common path for opening-grasping. The elimination of lower jaw opening after N.dm section, followed by the elimination of all jaw opening when section of the protractor quadrati nerve was added suggests that these 2 nerves compose the final common path for opening-grasping.

The conclusions regarding the role of M. protractor quadrati are subject to the cautions noted in Experiment 1, since they are based on the observation of external events. It should also be noted that opening of the maxilla following depressor mandibulae nerve section could represent a learned compensatory response to the absence of lower jaw opening. This is unlikely, however, since jaw opening was evident during the initial pecks following surgery.

It appears that the peripheral motor control of opening-grasping involves a relatively simple neural system, composed of two motor subnuclei. A simple motor system is a great advantage in attempting to unravel the sensorimotor control of any behavior since it limits the number of peripheral paths which must be followed into the CNS.

As noted above, the afferents to the jaw motor subnuclei (openers and closers) have been identified by Berkhoudt, Klein and Zeigler (1982). These subnuclei all receive inputs from the lateral parvocellular reticular formation, the trigeminal mesencephalic nucleus and the intertrigeminal area. Determining which of these areas are involved in opening-grasping would be a possible next step in the analysis of the efferent control of this response. This could be accomplished by determining the effect of lesions of each of these areas upon mouth opening. Once the involvement of a premotor area is established, electrophysiological methods could be used to map the neurons within that area which project to the jaw opener subnuclei (somatotopic organization).

General Discussion

As noted above, the eating response of the pigeon might represent a model system for the study of vertebrate ingestive behavior. Furthermore, the response provides a unique opportunity to study the interactions between motivation and motor control. This is apparent from the fact that lesions of any portion of a putative feeding circuit in the pigeon produce both motivational and sensorimotor deficits. The analysis of seed grasping suggests that the eating response may have yet another useful application, that is, for the study of vertebrate visuomotor behavior.

Although the two behaviors are morphologically different, they are functionally similar. During visually guided grasping in primates (see Lawrence and Kuypers, 1968; Jeannerod, 1981), the arm carries the hand to the vicinity of the target. This has been referred to as the transportation component. During the manipulation component, a finger grip or aperture is formed. In seed grasping by the pigeon, the neck carries the jaws toward the seed during the pecking component, while the gape or inter-jaw aperture is formed during the opening-grasping component. Therefore, in these two behaviors, the neck of the pigeon is the functional analogue of the arm, while the pigeons jaws are functionally analogous to the primate hand.

Studies of human visually guided grasping by Jeannerod (1981) reveal interesting similarities in topography and spatiotemporal organization between this behavior and seed grasping in the pigeon, which complement the functional similarities. Subjects were asked to grasp objects of different shapes and diameters (2 mm, 40 mm, 55 mm) placed 250-400 mm in front of them. The graph of position as a function of time for the transportation component (see Jeannerod, 1981, Figure 9.3) is basically similar to those for the pecking component of seed grasping (see Figures 25 and 26) in that both functions are sigmoid shaped. In comparing the velocity functions for the two behavioral components (see Jeannerod, 1981, Figure 9.3) (see Figures 27 and 28) it appears that both are basically curvilinear, however, the transition from acceleration to deceleration is much sharper for transportation than for pecking. This may be due to the fact that the breaking mechanisms for pecking must overcome the force of gravity as well as the muscle force which initiated the movement. It should be noted that the position and velocity functions for pecking are somewhat truncated since measurements were only recorded to the point where the beak was just above the seed, and not to substrate contact. Comparing Figure 9.3 of Jeannerod (1981) with Figures 27 and 28 also reveals somewhat similar peak velocities for the transportation (approximately 800 mm/sec) and pecking components (520-970 mm/sec). Furthermore, as for pecking, the velocity of the transportation component increases with distance from the object.

With respect to the manipulation and opening-grasping components, both appear to vary with object size. Grip size (inter-finger aperture) and gape size (inter-jaw tip aperture) both increase as the size of the target object increases. The same is true for the peak velocity of the two components. Furthermore, the magnitude of the peak velocity for manipulation (approximately 300-400 mm/sec, based on Jeannnerod, 1981, Figure 9.3) and opening-grasping (237-290 mm/sec, based on the milo and garbonzo means for two randomly selected birds) appear somewhat similar.

In addition to the functional and behavioral similartities between mammalian visually guided grasping and seed grasping in the pigeon, there are also similarities with respect to the neural organization and control of the 2 responses. In the pigeon, the occipitomesencephalic tract (OMT) originates from the anterior two-thirds of the archistriatum in the telencephalon (Zeier and Karten, 1971), and has a portion of its efferent connections terminating in the brainstem and spinal cord (Levine and Zeigler, 1981). Among its brainstem connections are cells in the lateral parvocellular reticular formation, which have been identified as premotor afferents to jaw motoneurons (see Berkhoudt, Klein and Zeigler, 1982). On the basis of its cytomorphology and connections, the archistriatum has been considered the avian equivalent of mammalian sensorimotor cortex (Zeier and Karten, 1971). Furthermore, it has been suggested that the OMT be considered a component of a set of pathways functionally equivalent to the mammalian pyramidal tract (Karten and Dubbledam, 1973).

Lesions of the OMT in the pigeon, and of the pyramidal tract in mammals respectively produce deficits in seed grasping and in visually guided reaching. In the pigeon, lesions of the OMT by Levine and Zeigler (1981) were found to produce deficits in both pecking and in opening-grasping. The effects upon pecking were reflected in the orientation of the head with respect to the position of the seed. In normal birds, most errors of orientation are equally distributed between the right and the left, with relatively few errors of overshoot or undershoot. Lesions of OMT result in a considerable increase in overshoot errors and a bias of left/right errors to one direction. The effects of OMT lesions on opening-grasping were reflected by deficits in the amount of gape. Normally, at substrate contact, gape is slightly larger than the diameter of the seed. OMT lesions reduce gape size for larger seeds such that inter-beak tip distance is actually smaller than the diameter of the seed, resulting in a striking of the seed by either the maxilla or mandible.

Lesions of the pyramidal tract in rhesus monkeys mainly effected the manipulation component. Between one and two days following bilateral section of the tracts the animals could reach "...with their arms towards food but their hands remained limply extended..." (Lawrence and Kuypers, 1968, p. 4). Up to 11 months after the operation, the animals could not perform individual movements of the fingers. The pyramidal tract in these animals appeared to control the speed and agility of movement as well as the fractionation of movement.

Pyramidal tract lesions in more primitive mammalian species such as rats and cats mainly effected the transportation component. Rats with unilateral pyramidal tract lesions showed no obvious impairment of digit flexion, however, they frequently dropped or missed food pellets when using the affected forelimb (Castro, 1972). These misses were a result of impairments in the orientation of the forelimb characterized by slight over- and underextensions with respect to the object. Edwards and Flynn (1972) observed the electrically induced striking behavior of cats with unilateral lesions of the pyramidal tract and found a disruption of the spatial organization of the response.

In addition to the functional, behavioral and anatomical similarities outlined above, there also appear to be similarities with respect to the sensorimotor control of mammalian visually guided reaching and seed grasping in the pigeon. As previously mentioned, distance from the object appears to influence the velocity of the transportation component, whereas the size of the object appears to influence the velocity of the manipulation component. A similar condition exists in the pigeon. Distance of the head from the seed determines the velocity of the pecking component, whereas the size of the seed determines the velocity of the opening-grasping component. It therefore appears that for each response, the efferent mechanisms which control the velocity of the individual components are under the control of different properties of the stimulus situation. This suggests the possibility of separate sensorimotor channels controlling the velocity of these components.

As outlined above, mammalian visually guided reaching and seed grasping in the pigeon have similarities in terms of function, behavior, neural control and sensorimotor control. These similarities suggest that seed grasping in the pigeon may be a useful system for the analysis of visuomotor control in mammals, in addition to its utility for the study of ingestive behavior. Although no bird has ever been the ancestor of a mammal, the brains of birds and mammals do not represent divergent directions of vertebrate evolution. In recent years, evidence for structural and functional homology in corresponding sensory and motor subsystems of these groups (Cohen and Karten, 1974; Hodos, 1976) has supported the validity of comparisons between them.

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