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EFFECTS OF DEAFFERENTATION OF THE OPHTHALMIC AND MANDIBULAR BRANCHES OF THE TRIGEMINAL NERVE AND NUCLEUS BASALIS LESIONS ON THE DIFFERENTIAL INGESTION OF SEEDS BY THE DOMESTIC PIGEON (Columba livia).

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EFFECTS OF DEAFFERENTATION OF THE OPHTHALMIC AND MANDIBULAR BRANCHES OF THE TRIGEMINAL NERVE AND NUCLEUS BASALIS LESIONS ON THE DIFFERENTIAL INGESTION OF SEEDS BY THE DOMESTIC PIGEON (*Columba livia*)

by

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Abstract

Experiments were conducted to determine the feasibility of using the pigeon's differential ingestion of seeds as a dependent variable to assess the role of the trigeminal "orotactile sense" in feeding behavior.

Pigeons offered two, three, or four different kinds of seeds ad libitum for 30 consecutive days showed a highly individualistic and variable but significant differential ingestion. While long term changes were seen, differential seed ingestion was relatively stable over time and under different methods of presentation and was largely unchanged after a 12-day period of restriction to a previously least eaten seed.

Birds reduced to 90%, 80%, or 70% of their ad libitum body weight showed an increased ingestion of small seeds and a decreased ingestion of large seeds relative to their previous ad libitum seed ingestion.

Peripheral deafferentation of the ophthalmic and mandibular branches of the trigeminal nerve and electrolytic lesions of nucleus basalis led to periods of aphagia, hypophagia and body weight loss. Upon the recovery of feeding after trigeminal lesions pigeons decreased the ingestion of small seeds and increased the ingestion of large seeds.

The results indicate that the sensorimotor deficits

which follow trigeminal damage disrupt the pigeon's characteristic differential ingestion of seeds.

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This thesis is dedicated to my father, David W. Moon, whose early guidance provided the foundation for this endeavor, and to my wife, Bonnie Jean, whose love and sense of humor smoothed the way.

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Regulatory systems have mechanisms for the detection of their contents and/or changes in content. Specialized cells which have detection as their function are commonly known as ". . . receptors, . . . sensory cells or . . . detectors" (Brobeck, 1965, p. 8). However, one must be cautious in stating exactly what is detected. Receptors seldom respond to all aspects of their content, but rather, respond only to those specific features of their content which have had an evolutionarily adaptive function (Brobeck, 1965).

In the case of body weight regulation, mechanisms exist for the "detection" of certain characteristics of food and/or changes in these characteristics. It is in this indirect way that food itself is detected.

Investigators in search of the neural mechanisms underlying the detection of food have attempted (1) to determine whether orosensory and/or postingestional feedback from food are requisite for the control of food intake and the regulation of body weight and (2) to define the specific location and _modus operandi_ of the food detection mechanisms and their function in the differential ingestion of foods. They have generally used one or more of the following techniques: (1) lesions have been placed in the central nervous system, primarily in the lateral or ventromedial hypothalamus; (2) lesions have been placed in the peripheral nervous system to decrease or prevent the orosensory and/or postingestional feedback which normally accompanies feeding (e.g., vagotomy; Snowdon, 1970); (3) oropharyngeal and other detection mechanisms have been bypassed by means of surgically produced fistulae which permit the direct introduction of food into selected regions of the digestive tract.

The results of studies using these methods have provided points of dissension for the historical and continuing controversy concerning the relative importance of central versus peripheral neural contributions to food intake (e.g., Grossman, 1967). However, collectively these studies show that there is a great redundancy of mechanisms which insure food intake and that there are interrelationships between the neural mechanisms responsive to food quality (or kind) and to food quantity (e.g., Teitelbaum & Epstein, 1962).

Rationale for Studies of the Orosensory Control of Food Intake of the Pigeon (*Columba livia*)

This redundancy of neural mechanisms has presented challenging technical problems to researchers seeking to experimentally dissociate peripheral and central contributions to the sensory control of food intake. These problems have, in large part, been met with indirect methods, primarily the use of fistulae and/or operant techniques (e.g., Teitelbaum, 1964). As an alternative approach to the problems presented by redundancy, investigators have used species with specific morphological and physiological features which facilitate the experimental dissociation of peripheral and central contributions. The organisms chosen for study may possess fewer neural elements and therefore less redundancy (e.g., the blowfly; Dethier, 1969) or may, as in the case of the pigeon, possess unique neuroanatomical features. The pigeon has an oral anatomy which permits the direct deafferentation of the ophthalmic and mandibular trigeminal branches without the disruption of motor function (Zeigler, 1974b). In addition, several studies by Zeigler and Karten (1973a, 1973b; See Zeigler, 1974a) have provided an understanding of the anatomical relationships between these trigeminal sensory branches and neural structures related to feeding behavior that lie within the pigeon's central nervous system. These anatomical studies by Karten and behavioral studies by Zeigler have used inbred strains of Columba livia because it was these strains, obtained from the Palmetto Pigeon Plant, that were used in the preparation of the atlas of the pigeon brain (Karten & Hodos, 1967). Strains of Columba livia obtained from this source may be expected to have anatomical features which approximate those shown in the atlas.

Mature birds obtained from the Palmetto Pigeon Plant have been maintained on different kinds of grains presented in a four grain *ad libitum* "cafeteria style" feeding regimen (Personal communication, 1973; Levi, 1963). It is not known to what extent their differential ingestion of seeds reflects that which might be found for feral *Columba livia*. The problems associated with extrapolating from laboratory studies of the feeding of this strain to the feeding behavior of *Columbids* under field conditions are discussed in Zeigler, Green, and Lehrer (1971).

The Pigeon's Feeding System and the Trigeminal Orotactile Sense

Zeigler (1974a) has extensively analyzed trigeminal afferent neural structures controlling food intake and body weight regulation in the pigeon. He and his associates have defined a series of trigeminal structures at several levels of the pigeon's brain properly called a "feeding system" (Figure 1). This system begins with the three peripheral branches of the trigeminal nerve subserving an orotactile sense. These afferent fibers, whose cell bodies lie within the Gasserian ganglion, are served by axons directed centrally toward the principle sensory (PrV) and spinal trigeminal nuclei (TTD). PrV is, in turn, the origin of second order neurons, axons of which ascend bilaterally as the quinto-frontal tract (QFT) to synapse in the nucleus basalis (NB) which lies in the basolateral

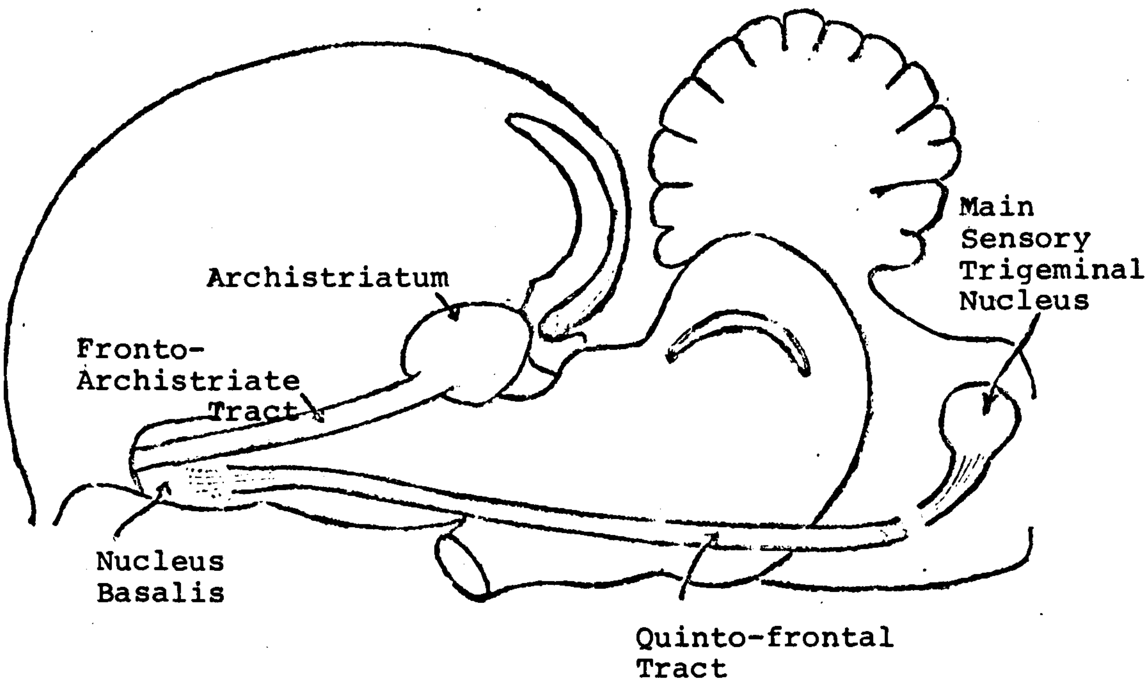


FIG. 3. Schematic representation of major neural structures in the trigeminal feeding system.

anterior telencephalon. An NB efferent, the fronto-archistriate tract, terminates in the archistriatum, portions of which have fiber connections with both the hypothalamus (via the occipitomesencephalic tract pars hypothalami and the stria terminalis) and extrahypothalamic motor areas.

The major afferent structures of this feeding system, i.e., the three branches of the trigeminal nerve, PrV, QFT, and NB, have been investigated by a variety of methods which have provided an understanding of the anatomy of this system and its role in the neurosensory and motivational control of food intake and the subsequent maintenance of body weight (Zeigler, 1974a).

The three afferent branches of the pigeon's trigeminal nerve innervate the orbit, beak, and oral cavity but not the tongue (Kitchell, Strom & Zotterman, 1959; Witkovsky, Zeigler & Silver, 1973). The ophthalmic and maxillary branches distribute to the upper beak and the mandibular branch lies within a narrow medio-lateral recess extending the length of each side of the lower beak (Figure 2). Electrophysiological recordings from TTD (Silver & Witkovsky, 1973), PrV (Zeigler & Witkovsky, 1968) and NB (Witkovsky, et al., 1973), have shown at least two major cell functions. Large numbers of the cells in these nuclei are activated by probing (i.e., tactile stimulation)

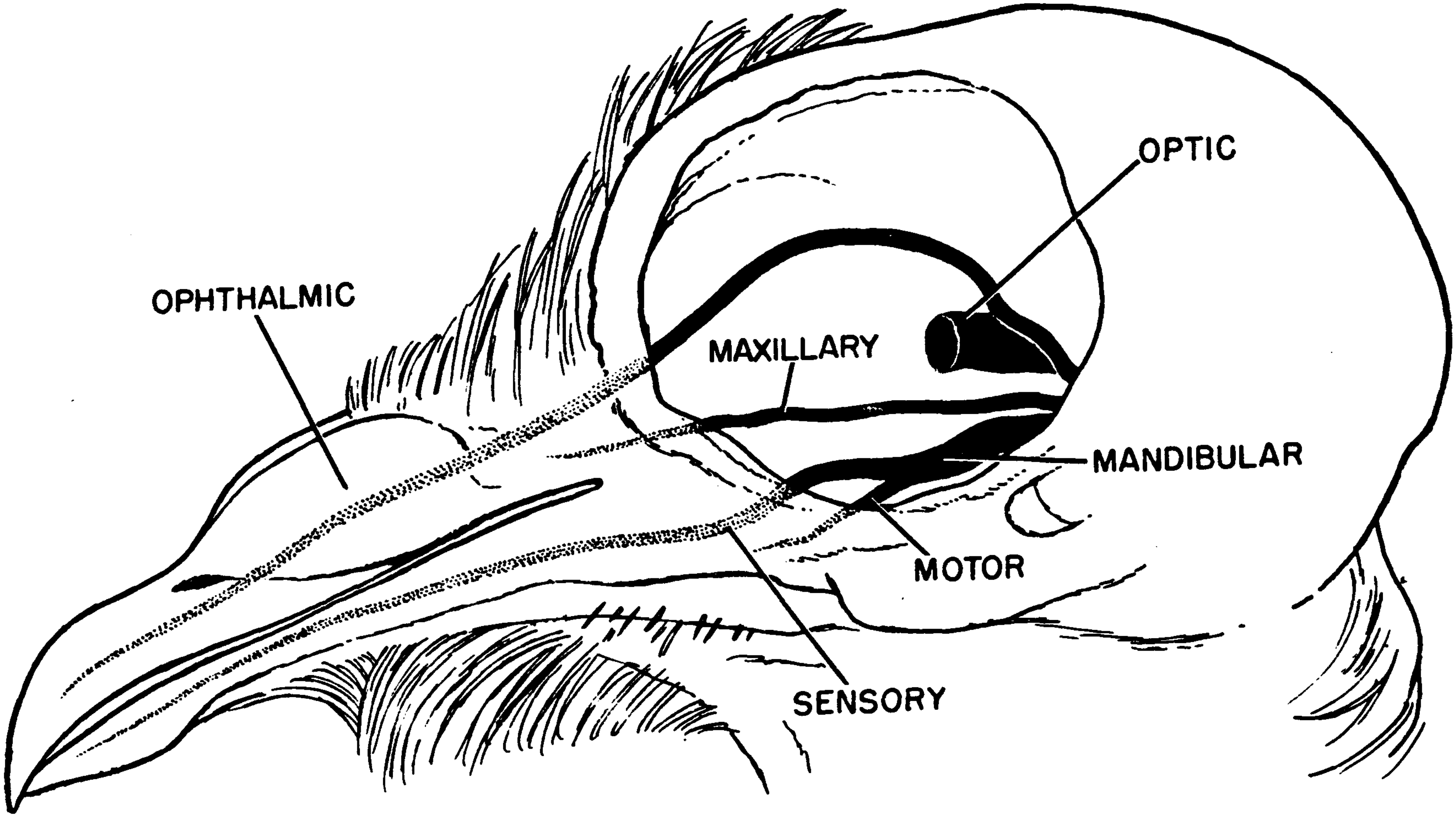


FIG. 2. Gross dissection showing the ophthalmic, maxillary and mandibular branches of the pigeon's trigeminal nerve (From Zeigler, 1974b).

the beak and oral cavity or the feathers of the neck, head, and orbital region. Other cells are responsive to the angular displacement of the upper and lower beak. Tactile receptive fields are found both on the rim of the beak and on the soft palatal tissues within the oral cavity which parallel the beak rim. A few receptive fields were found on adjacent portions of the upper and lower beak tips.

Collectively, these results suggest that mechano- or tactile receptive fields on the beak and within the oral cavity, which are served by the three trigeminal branches may "... signal the presence of a kernel of grain at the beak tip and provide complementary information about its static position and movement within the mouth, and signal opening and closing of the mouth" (Zeigler, 1974a, p. 122).

They further suggest that the orotactile sense subserved by the trigeminal branches and "feeding system" may provide the primary sensory basis for the maintenance of a differential ingestion of seeds consistent with previously developed associations between the visual characteristics of different seeds and their respective orotactile and postingestional qualities. Surgical procedures which remove or damage the major trigeminal afferents, and subsequently change the pigeon's general responsiveness to food (Zeigler & Karten, 1973b), may also alter the differential ingestion of foods.

The experiments described below were designed to test the hypothesis that orotactile stimulation derived from, and perhaps specific to, different kinds of seeds, provides a primary sensory basis for the pigeon's differential ingestion of seeds and that surgical intervention in the trigeminal "feeding system" should alter or disrupt the trigeminal orotactile sense and thus change the pigeon's differential ingestion of seeds.

The first set of experiments provide the rationale for making comparisons of the pigeon's differential ingestion of seeds before and after trigeminal damage. This was necessary because this measure (i.e., the differential ingestion of seeds) had not been previously used to define the effects of damage to the peripheral and central nervous system.

The second set of experiments investigates the effects of deafferentation of the mandibular and ophthalmic branches of the trigeminal nerve and of electrolytic lesions of the nucleus basalis on the pigeon's differential ingestion of seeds.

II

General Methods and Procedures

Subjects and Their Maintenance

The subjects were male and female White Carneaux Pigeons (*Columba livia*), 2-6 years old, purchased from the Hillside (birds 9, 13, 20, 23, 335, 381, 382) and Palmetto (all other birds) Pigeon Plants.

As all birds showed a highly individualistic differential ingestion of seeds irrespective of their source and plant designated age and sex, and because previous studies have shown that gender is not a significant variable in neurobehavioral studies of feeding (e.g., Zeigler, 1974a) these characteristics are not indicated in the remaining sections of this report.

The birds were individually caged within a colony room and maintained on "Columbia Special" seed mixture (See below) *ad libitum* during an adjustment period of at least 30 days prior to treatment. Tap water was available *ad libitum* from 250 ml graduated glass watering tubes. Ambient temperature was 70^{o}-80^{o}F and a 15-hour light/dark cycle (8 a.m. - 11 p.m.) was in effect at all times.

Foods

The advantages of using commercially pelleted crushed seeds and unaltered whole seeds were assessed in several pilot experiments. Pelleted crushed seeds of guaranteed nutritional content (45 mg Noyes Pigeon Pellets) were found unsatisfactory for the following reasons: (1) their physical characteristics, and therefore, their orotactile qualities were changed because the birds' pecks ground them into a fine powder; (2) their very different appearance (e.g., greyish-white color) relative to the whole seeds which the birds were previously fed at the pigeon plants appeared to be the basis for very different degrees of initial acceptance; (3) their appearance had to be changed in some manner to provide several distinctly different "kinds" of food. The basis of the pigeon's differential ingestion of foods was not known. Therefore, it was not possible to readily alter the characteristics of the pellets so that they would vary along the "typical" continua of these unknown dimensions. The bases for a differential ingestion of "altered" pellets could be very different from those associated with the differential ingestion of the seeds in a bird's previous diet.

The pilot experiments conducted with several kinds of whole seeds commonly used as pigeon food (Levi, 1963) indicated that their physical appearance and other characteristics were much more stable than those of the commercially prepared pellets. Birds showed a highly individualistic differential ingestion incompatable with an hypothesis that they were ingesting seeds on the basis of nutritional value. These observations were similar to those of Brown (1969) who found that pigeons fed whole seeds were highly individualistic in their "selection" and ate constant ratios of large and small peas (which were presumed to be of the same nutritional quality).

Whole seeds were used in all subsequent experiments. Several different kinds of commonly fed (Levi, 1963) and available (Animal Feeds, Inc., NYC) seeds were chosen which would provide an adequate two, three, or four seed diet for pigeons (See Table 1). Available evidence suggested that any one of these seeds could maintain a pigeon's health for at least several weeks (Levi, 1963). All seeds were stored in a refrigerator at approximately 36^{o}F and then were kept in covered polyethelene containers at room temperature at least 24 hours prior to use.

"Columbia Special" seed mixture (50% milo, 40% vetch, 10% hemp), the standard maintenance diet for the colony, was fed prior to treatments. Then, corn(C), hemp seed(H), kafir(K), maple peas(P), or vetch(V) were offered in different combinations which varied in number, size, and "palatability" for the following reasons:

Table 1

Characteristics of Seeds Presented to Pigeons

	Common Name					
	Corn	Vetch	Hemp	Kafir	Maple Peas	Milo
Genus	Zea	Vicia	Cannabis	Sorghum	Pisum	Sorghum
Species	mays	sativa	sativa	vulgare	sativum	vulgare
Shape	round	round	tear drop	tear drop	round	tear drop
Color	yellow	black	green	white	brown	rust
Size	5-14mm	3-4mm	3-5mm	2.5-4mm	5-8.5mm	2.5-5mm
Seeds/Gram[a]	4.0	17.9	48.0	41.8	3.9	41.6
<u>Composition</u>						
Water	14.8%	-	8.8%	11.4%	10.8%	10.6%
Protein	9.4%	37.0%	21.5%	11.2%	25.3%	11.2%
Fat	3.9%	2.5%	30.4%	3.0%	1.7%	2.9%
Fiber	2.2%	3.5%	18.8%	2.3%	5.7%	2.2%
Nitrogen Free Extract	68.4%	-	15.9%	70.3%	53.6%	71.2%
Mineral Matter	1.5%	-	4.5%	1.7%	2.9%	1.9%
Digestibility	80.6%	80.0%	-	80.1%	78.4%	79.9%

[a]Seeds/gram is the mean of five 10 gram samples. Composition values taken from Levi (1963). Values presented are for the wrinkled variety of peas.

(1) Kafir and peas were offered in two grain presentations because of their different sizes. It was thought that sensorimotor deficits might be more evident in the ingestion of the smaller seeds;

(2) Hemp was fed with kafir and peas in three grain presentations because it was only slightly larger than kafir but was known to be avidly accepted ("highly palatable") by pigeons (Levi, 1963). This combination provided for the dissociation of potential postsurgical changes in ingestion related to sensorimotor deficits in feeding and "finickiness" or an enhanced sensitivity to orosensory quality;

(3) Corn, kafir, peas, and vetch were fed in four grain presentations. This provided for the same dissociations of sensory deficit and "palatability" under conditions which offered a greater variety of sizes and textures;

(4) Corn, hemp, peas, and vetch provided a continuum of seed size and another condition which offered a variety of sizes and textures.

The percentages for nutrients and digestibility shown in Table 1 are only approximations because they were obtained in feeding trials with Columba palumbus or other species of animals (Levi, 1963). Pigeons are seldom used in feeding trials (Murton, Isaacson, & Westwood, 1963) but studies of other avian species (Willson & Harmeson, 1973) have shown that: (1) there may be great interbird variability in the values obtained for the digestibility of a given kind of seed; (2) the same bird may show very different values for a given kind of seed on different feeding trials; and (3) the digestive efficiency of a given seed may be greater when greater amounts of one kind of seed are eaten; however, this is not true for all birds within a test.

The seeds offered in the present study were common pigeon foods chosen for their nutritional characteristics, so that restriction to any one seed or combination of seeds would not produce deficiencies. As the available values for nutrients and digestibility were approximations, the present study was not designed to provide information concerning the nutrient intake of each bird. Therefore, the intake of specific nutrients was not analyzed.

Feeders

The seeds were presented in clear plastic troughs 1 3/4" high and 4 1/2" long. The width of these troughs varied from 2 1/2" to 1 1/2" for the two to four grain presentations. Trough sets were held in a clear plastic rectangular enclosure 4" wide, 4" long, and 8 1/2" high which was attached to the front of each cage approximately 5" from the watering tube.

Procedures for the Feeding Regimen

The birds were permitted to eat from several troughs each of which contained 40 grams of a different kind of seed. This quantity was sufficient to assure that no one kind of seed was totally consumed.

The location of each kind of seed was changed daily, from one trough to the next in a round-robin fashion, so that each kind of seed occupied each trough position within the feeder an equal or nearly equal amount of time, every N days, where N is the number of different kinds of seeds presented. Most birds were fed three different kinds of seeds. Thus, measures of seed ingestion were most frequently taken for periods of 12, 15, or 30 consecutive days before and after treatment and therefore provided four, five, or ten measures for each seed/position combination.

Experiments designed to describe the effects of food deprivation and the effects of restricting feeding to a previously least eaten seed required other regimens which are presented in respective sections below.

Procedures for Measuring Seed Ingestion

Unless otherwise noted, seed ingestion was measured daily between 10 a.m. and 2 p.m. while the subjects were maintained on the above feeding regimen. Spilled seeds were recovered from cardboard beneath the cage, separated and weighed with the remaining amount of the same kind of seed to the nearest .5 grams on a Mettler balance. The difference between the weight of the seed remaining and 40 grams, the weight of the seed placed in each trough the previous day, was recorded as the amount of the seed eaten on the previous day. Fresh seeds were then added to the remaining seed until the combined weight was 40 grams. The seeds were placed in the next trough position within the feeder box. When the seeds had been measured for all subjects the feeder boxes were returned to the front of the cages.

Procedures for Measuring Water Intake and Body Weight

Water intake was measured each day in the following manner: the amount of tap water remaining in each bird's graduated watering tube was subtracted from 250 mls. This difference was recorded as the water intake for the previous day; the watering tube was refilled with 250 mls. of fresh tap water, and the tube was replaced on the front of the cage.

Each bird was weighed ($\pm$ 1g) every other day on an Ohaus balance scale.

Statistical Procedures

The significance of differences between all pre- and posttreatment measures were analyzed for individual subjects by computing Kruskal-Wallis Analyses of Variance and/or Mann-Whitney U Tests on the raw data. Differences in the relative amounts of different kinds of seeds eaten before and after treatment were tested with Friedman Analyses of Variance and/or Wilcoxon Matched Pairs Tests.

Differences between the pre- and posttreatment measures for subjects within groups were tested with Wilcoxon Matched Pairs Tests, Randomization Tests for Matched Pairs, or Binomial Tests (Siegel, 1956). The data from different groups were compared using Mann-Whitney U Tests as described in respective results sections below.

All statistical tests were two-tailed and were conducted at the .05 level of significance. They were, except where noted, computed with the assistance of a programmable calculator (Hewlett-Packard 9810) which provided test statistics and normal deviates ("Z scores") the significance of which were determined using the tables in Siegel(1956). Programs for the ranking of data and for Mann-Whitney, Friedman, and Wilcoxon Tests were published by Hewlett-Packard, Incorporated. The program for the Kruskal-Wallis Analyses of Variance was developed by Dr. Lester R. Aronson, Department of Animal Behavior, The American Museum of Natural History, New York, where the research was conducted.

III

Experiments Relating to the Differential Ingestion of Seeds by Pigeons

Control of Potential Ingestants

Examination of the literature concerned with the proportions of different foods eaten by mature birds shows two general kinds of investigations. First, there are many naturalistic studies which report observations of feeding birds or analyses of the stomach contents of shot birds. While these studies have shown correlations between morphology and specific ingestive habits and have frequently described seasonal variations in diets they have frequently failed to quantify the proportions of potential ingestants available. Second, there are a smaller number of papers which report the proportions of foods eaten in laboratory or field studies in which the potential ingestants have been carefully controlled or assessed (See Schoener, 1971). A number of these are described as studies of predation, food choice or "preference" depending on the author's emphasis (e.g., Krebs, 1973).

The Concept of "Preference"

The concept "preference" used in these studies indicates that the frequency of responses toward, or grams or percent intake of certain kinds of foods is statistically, or absolutely greater than others, or, that a significant or large proportion of a population shows similar ingestive responses. The failure to distinguish between statistically different relative intake and absolutely, but not statistically different relative ingestion, has greatly limited the usefulness of the term "preference". Its utility has been further diminished by a failure to use terminology consistent with distinctions which could be made between the very different experimental treatments whose results are all called "preferences." This confusion of terminology and operations has been a source of contradiction arising in studies of differential ingestion (Pfaffmann, 1969; Irwin, 1971).

Differential Food Ingestion by Chickens

Some investigators have measured feeding behavior directly while others have measured the proportions of different foods eaten. The latter method has been used when individually or group caged chickens have been studied to determine (1) the developmental bases of food "selection" (e.g., Dove, 1935), (2) the role of specific sensory systems in guiding differential ingestion (Gentle, 1971), or (3) "preferences" for specific sensory characteristics of foods (e.g., Hurnik, Jerome, Reinhart & Summers, 1971).

At this time, no one sensory characteristic of food has been shown to be the basis of the differential ingestion of nutritionally replete foods by chickens. This may be because differential ingestion is usually based on several sensory qualities of foods (Gentle, 1973). However, it could indicate that the sensory modality(ies) critical for the orosensory control of the differential intake of foods has (have) not been found or has (have) not been sufficiently investigated. The results from studies which have used chickens as subjects cannot be generalized to the pigeon or to the conditions in the present experiments because: (1) chickens are precocial and omnivorous while pigeons are altricial and gramnivorous and (2) studies which have used chickens as subjects have frequently used liquid, or commercially produced pellets or mash rather than whole seeds.

Seed Ingestion of Captive Wild Birds

A number of studies were found scattered throughout the agricultural, biological and ornithological literature concerning the differential seed ingestion of captive wild birds. The studies of Kear (1962), Willson (1972), Willson and Harmeson (1973), and of Ligon and Martin (1974) are relevant to the present study because they indicate several different variables which might lead to a differential ingestion of whole seeds.

Kear (1962) studying the interspecific differences in the seed ingestion of seven species of captured wild British Finches found that the ad libitum ingestion of canary, millet, rape, hemp, linseed, and sunflower seeds changed over a 12-day period from a high intake of small seeds (canary, millet, rape) to a high intake of larger seeds (hemp, sunflower). While species differed in the proportions of seeds they ingested, all but one species took all seed types and only two of the seven species failed to take more hemp than any other seed. Two linnets receiving these same six seeds for six months showed a 60% decreased consumption of small seeds (from 80% to 20%) and a comparable increase in the ingestion of hemp. Seed "ingestion" was also analyzed in relationship to bill morphology, seed husking efficiency, nutritive content, seasonal changes and dietary experience (restriction to one type of seed or to a seedless diet).

It was concluded that interspecific differences in seed ingestion were a major factor reducing competition between different species feeding at a single food source. These interspecific differences in seed ingestion were related to bill size in that large billed species changed their ingestion from small to large seeds more rapidly than birds with smaller bills over a 12-day period. Bill structure, bill size and the nature of the seed husk were important determinants of interspecific differences in seed ingestion.

Willson (1972) reported that captive (wild) Cardinals frequently did not show "size preferences" when eating sunflower and hemp seeds, presumably because their large beaks could husk both large and small seeds. Tree and Song Sparrows, Slate-colored Juncos, Purple Finches, and Rose-Breasted Grosbeaks usually ingested large numbers of small (short and thin) sunflower seeds presumably because they had difficulty managing the larger seeds. In a more recent study, Willson and Harmeson (1973) found that Cardinals offered six different kinds of seeds ingested greater numbers of large seeds although all birds sampled every type of seed offered and no one of the six different kinds of seeds was eaten in a quantity which was less than 10% of the total diet. Cardinals consistently ingested large numbers of seeds of intermediate or low caloric content/gram and did not eat to maximize caloric content/kernel, potential caloric intake/unit of time, or protein or lipid intake.

Ligon and Martin (1974) observed that Pinon jays feeding on seeds of the pinon pine ingested only those seeds which contained a healthy endosperm. Subsequent laboratory experiments with wild jays indicated that "bad" seeds (i.e., those which had no endosperm) were not picked up, were briefly picked up in the bill and dropped, or were picked up and then dropped from the beak only after a period in which the mandibles rapidly opened and closed on the seed. Experiments which altered the visual, gustatory, and tactile qualities of pinon seeds suggested that olfactory and gustatory cues were not used but that the tactile stimulation related to the weight of the seeds and auditory cues provided by the mandibular movements and visual differences were used to discriminate "good" from "bad" seeds.

Collectively, these laboratory studies with captured, wild birds suggest that: (1) the ingestion of seeds follows discriminations based on multidimensional cues; birds do not ingest seeds on the basis of only color, taste, etc.; (2) behavioral prerequisites such as husking or other preparations may be an important determinant of the differential ingestion of seeds; and (3) the avian species studied generally do not eat a single kind of food and will eat some of each of several different kinds of seeds presented simultaneously.

Seed Ingestion of *Columba livia* and *Columba palumbus*

Relatively little is known about the pigeon's differential ingestion of seeds. Only three investigators have reported significant studies on individual pigeons.

Brown (1969) has completed the only previous thorough study of individually caged domestic pigeons (*C. livia*). He offered 59 pigeons in an unheated room a 25-gram mixture containing 5 grams each of the five kinds of seeds found in Purina Mixed Pigeon Seed for 3 hours immediately following 40 hours of food deprivation. The combined results of two 3-hour tests showed great individual differences. Some pigeons ate large amounts of the seeds rejected by the majority of birds. Mean square analyses showed that seed ingestion changed uniformly from the first test to the second with all birds tending to change in the same direction. Analyses of relative availability showed there was no correlation between ingestion and seed weight, percent by weight, or frequency of occurrence, in the Purina Mixture. Individual patterns of seed ingestion were not correlated with bill size. When 10 grams of each seed was presented instead of 5 grams, the proportions of the different seeds ingested remained the same but total food intake increased. Birds offered two sizes of the same seed ingested a constant ratio of these two sizes instead of maximizing calories/seed by ingesting only the larger.

Murton has reported that: (1) young wood pigeons (*C. palumbus*) show seed "preferences" before leaving the nest which persist after a 3-month exposure to commercial poultry pellets; (2) pigeons eat their "most preferred" seeds first, then the second "most preferred," etc.; and (3) pigeons generally eat in flocks that are affected by the density of a given food (seeds/unit area) in a manner that departs from that predicted by mathematical models related to the concept of the "search image," i.e., the amount of a type of seed eaten is not correlated with the probability of encounters (1971). Murton's laboratory observations with captured wood pigeons suggested that wheat, maple peas, and peanuts were "most preferred;" green peas were second; hemp and maize were third; and millet rice, rape, mustard, linseed, and sunflower were "least preferred" (1965, p. 87). However, statistical analyses and data are not presented to support the statements concerning such "preferences."

Mathiasson's field observations (1967) suggested that Swedish wood pigeons (C. palumbus) are "monophagously inclined" but responsive to the increased variety of foods that become available from July to October. They are "selective" in their "choice" of acorns choosing the medium-sized acorns first, and then larger or smaller ones. Transitions from eating one kind of food to eating another may occur either with the exhaustion of one food source or with the maturation of a second source prior to exhaustion of the first.

Mathiasson's experiments with one caged (wild) wood pigeon (1967) showed that the pigeon, after a period of time with only one kind of food, ate this food rather than others offered simultaneously. This occurred successively for barley, acorns, and green peas. He observed the same phenomenon with different colors: barley stained five different colors (yellow, black, green, red, and blue) was offered after a period of restriction to one color, and the "adapted color" was eaten.

<u>Orotactile Contributions to Differential Ingestion</u>

These studies with pigeons and several other species suggested that the simultaneous presentation of seeds would lead to a differential ingestion which, at least in some cases, would appear to be based on the size and tactual qualities of the seeds presented. Studies of the pigeon showing that the trigeminal system contains single units responsive to angular displacement of the beaks and to tactile stimulation on and within the beak (See Section I), suggested that trigeminal stimuli might play a more important role in the pigeon's differential ingestion of seeds than olfactory and gustatory stimuli (Zeigler and Karten, 1973b). This hypothesis was supported by studies showing that trigeminal damage in pigeons led to aphagia and/or hypophagia (e.g., Zeigler, 1974a). The evidence above suggested that the characteristics of the pigeon's differential *ad libitum* ingestion of seeds might permit another means of testing this "orotactile hypothesis." Accordingly, the first experiment was conducted to assess the characteristics of the pigeon's *ad libitum* ingestion of several kinds and numbers of seeds. The results provided a basis for choosing specific experimental dependent variables.

III A

Characteristics of the Pigeon's *ad libitum* Differential Ingestion of Seeds

As there were no long term studies of feeding behavior in individually caged *Columba livia*, the nature of the pigeon's seed ingestion could not be readily predicted. Therefore, a body of data was collected to show the reliability of the characteristics of individual pigeon's seed ingestion over a period of 30 days. This length of time was thought sufficient to monitor the effects of different kinds of experimental treatments whose effects might be observed only over an extended period of time. These observations also served to demonstrate the feasibility and desirability of using the differential ingestion of seeds as a dependent variable. As it was well documented that ingestive patterns vary with different methods of presentation (e.g., Pfaffman, 1969), and as there was no *a priori* reason to believe that one method of presenting the seeds would yield data more reliable than another method, seed ingestion data were collected under several experimental conditions which differed in the number and kinds of seeds offered.

Methods and Procedures

Subjects

The subjects used in this experiment were 28 male and female White Carneaux pigeons randomly assigned to three groups maintained on different diets for 30 consecutive days.

Procedures

One group of five birds was fed only kafir and peas. A second group of 19 birds was fed hemp, kafir, and peas. The third group consisted of four birds fed corn, kafir, peas and vetch. All other experimental conditions were as described in Section II.

Results

The characteristics of the data for the daily intake (g) of each of the different kinds of seeds indicated that medians were the best measure of central tendency. Tables 2, 3, and 4 show the medians and ranges for the two, three and four grain presentations. There is a considerable range of values for the daily intake of each of the different kinds of seed. Also, the birds within each of the groups are highly individualistic in their seed ingestion. In two grain presentations all birds ate some of each of the two grains while 15 of the 19 birds fed three grains ate only two of the three grains. Only one of the four birds given four grains ate some of each seed and two birds

Table 2

Medians and Ranges for Kafir and Peas Intake(g) in 30 Daily Two Grain Presentations

Bird Numbers	Kafir		Peas	
	Median	Range	Median	Range
310	13.8	5.5-22.0	23.3	14.0-32.5
395	13.2	2.5-27.5	11.0	6.0-31.0
398	15.3	2.0-21.0	14.8	9.0-20.5
405	22.3	17.0-26.5	6.7	1.5-10.0
411	27.5	21.0-34.0	13.5	11.0-19.0

Table 3

Medians and Ranges for Hemp, Kafir, and Peas Intake(g) in 30 Daily Three Grain Presentations

Bird Numbers	Hemp Median	Hemp Range	Kafir Median	Kafir Range	Peas Median	Peas Range
9	10.2	3.5-16.5	14.8	6.0-20.5	*	
13	9.9	4.5-15.0	11.3	5.0-19.0	*	
20	14.2	9.0-29.5	11.3	1.0-18.0	*	
28	12.7	1.0-22.0	18.0	3.0-25.0	*	
316	15.8	10.0-27.0	13.8	3.0-21.0	*	
329	8.8	4.0-16.0	23.8	14.0-32.0	*	
333	10.8	0.5-18.0	14.8	9.0-20.5	*	
335	14.3	10.0-28.5	9.9	5.0-19.0	*	
341	12.8	4.0-19.5	18.5	4.0-25.5	*	
354	12.2	7.0-24.0	11.5	5.0-24.0	*	
365	9.3	4.0-19.0	15.0	6.0-21.0	*	
369	*		19.3	7.0-23.0	10.5	7.0-24.0
370	*		9.1	5.5-21.0	19.8	9.0-28.0
376	*		22.0	14.0-28.0	7.0	3.0-16.5
377	6.5	3.0-15.0	14.0	3.0-22.0	4.0	0.0-17.0
381	12.8	8.0-25.0	16.0	7.0-26.0	0.6	0.0- 7.0
382	9.9	4.0-14.5	14.8	9.0-23.0	*	
507	12.3	7.0-24.5	8.5	2.0-19.5	13.3	6.0-23.0
526	3.8	0.0-15.0	13.0	5.0-20.0	21.5	17.0-31.0

Note. Asterisks indicate a seed was not eaten.

Table 4

Medians and Ranges for Corn, Kafir, Peas and Vetch Intake(g) in 30 Daily Four Grain Presentations

Bird Numbers	Corn		Kafir		Peas		Vetch	
	Median	Range	Median	Range	Median	Range	Median	Range
306	9.8	4.5-20.0	6.8	0.0-15.5	3.0	0.0-11.0	7.3	2.5-15.5
392	*		11.3	6.0-21.5	*		13.0	6.0-20.5
393	10.6	4.5-16.0	10.7	7.5-14.0	*		7.3	5.0-17.0
394	10.2	5.0-16.0	6.8	3.5-13.0	*		13.8	11.0-19.0

Note. Asterisks indicate a seed was not eaten.

ate two of the four kinds of seeds. The highly individualistic seed ingestion within each of these groups required statistical analyses of each bird's intake, the results of which are shown in Tables 5, 6, and 7.

<u>Two Grain Presentations</u>

There was no significant difference in the intake of hemp and kafir for the group fed two grains (Binomial test, $p>.05$). However, inspection of the medians for hemp and kafir intake suggested that several birds did not ingest an equal amount of these grains (Table 2). Statistical analyses indicated that birds 405 and 411 ate more peas, bird 310 ate more kafir, and birds 395 and 398 ate equal amounts of these two grains (Table 5).

<u>Three Grain Presentations</u>

Significantly more birds ingested only two of the three kinds of grains, fewer birds ate peas, and more birds ate hemp than predicted by the null hypothesis (Binomial tests; $p=<.02$, $<.04$ and $<.01$, respectively). The group as a whole ate significantly more kafir than hemp and peas (Table 6). All of the birds ate kafir, 17 birds ate hemp, but only seven birds ate peas. In spite of the fact that almost twice as many birds ate hemp as peas, Wilcoxon tests computed on the median hemp and peas intake were not significant for the group. Statistical analyses computed on the seed ingestion of each of the three subgroups of birds (Table 6)

Table 5

Wilcoxon Tests on Seed Ingestion Data in Two Grain Presentations

Grains Eaten[a]	Bird Numbers	Relationship	*p*
KP	405	P>K	<.001
	411	P>K	<.001
	310	K>P	<.001
	395	K=P	>.20
	398	K=P	>.70
	Group	K=P*	

[a]K=kafir, P=peas
*Median test; p<.05

Table 6

Friedman and Wilcoxon Tests on Seed Ingestion Data in Three Grain Presentations

Grains Eaten[a]	Bird Numbers	Relationship	$\underline{p}$ Friedman	Wilcoxon
HKP	377	K>H>P	<.01	<.01;<.05
	381	K=H>P	<.001	>.10;<.001
	507	H=P>K	<.01	>.05;<.005
	526	P>K>H	<.001	<.001;<.001
	Subgroup	H=K=P	<.90	
KP	369	K>P		<.05
	376	K>P		<.001
	370	P>K		<.001
	Subgroup	K=P*		
HK	9	K>H		<.001
	329	K>H		<.001
	333	K>H		<.005
	365	K>H		<.005
	382	K>H		<.001
	20	H>K		<.01
	316	H>K		<.01
	335	H>K		<.001
	13	H=K		>.05
	28	H=K		>.40
	341	H=K		>.05
	354	H=K		>.80
	Subgroup	K>H*		
	Group	K>P=H	<.001	<.001;>.05

[a]H=hemp, K=kafir, P=peas
*Median Test; p>.05 for KP, p<.01 for KH

Table 7

Friedman and Wilcoxon Tests on Seed Ingestion Data in Four Grain Presentations

Grains Eaten[a]	Bird Numbers	Relationship	*p* Friedman	*p* Wilcoxon
CKPV	306	C>V=K>P	<.001	<.05; >.70; <.001
CKV	393	C=K>V	<.01	>.20; <.001
	394	V>C>K	<.001	<.001; <.001
KV	392	K=V		>.05
	Group	K=C=V=P	>.05	

[a]C=corn, K=kafir, P=peas, V=vetch

indicated that only the largest subgroup, which consisted of birds eating kafir and peas, ingested significantly different amounts of the seeds offered. Each of the subgroups contained birds which showed a highly individualistic and significant differential ingestion of seeds.

Four Grain Presentations

Only bird 306 ate some of each of the four kinds of seeds offered. Birds 393 and 394 ate corn, kafir, and vetch and bird 392 ate only kafir and vetch. An analysis of variance indicated there was no group difference in the ingestion of the four seeds even though all birds either ate less peas than other seeds or did not eat peas.

The Variability of Differential Ingestion

The variability in the daily intake of seeds is seen directly in the data for birds given two and three grains shown in Table 8. It is seen that both total intake and the intake of each seed shows considerable variability over days and that different proportions of seeds may be ingested even when total intake is approximately the same as is seen on days 6, 9, 11, 15, 16, 25, and 28 for bird 310. However, there are different patterns in the relationship between pairs of grains. Bird 376 consistently ingested more kafir than peas, while bird 310 ingested more kafir than peas only until the 23rd day. Bird 369

Table 8

Kafir and Peas Intake(g) of Birds 310, 369, and 376 on 30 Consecutive Days

	#310[a]			#369			#376		
Days	Kafir	Peas	Total	Kafir	Peas	Total	Kafir	Peas	Total
1	32.5	12.0	44.5	24.0	7.0	31.0	16.5	21.0	37.5
2	22.0	5.5	27.5	10.0	21.0	31.0	16.5	18.5	34.5
3	30.0	14.0	44.0	11.0	20.0	31.0	8.5	19.5	28.0
4	26.5	14.5	41.0	18.0	8.0	26.0	11.5	17.0	28.5
5	25.0	12.0	37.0	10.0	21.0	31.0	8.0	19.0	27.0
6	26.0	10.0	36.0	11.0	22.0	33.0	5.0	22.0	27.0
7	25.0	14.0	39.0	18.5	7.5	26.0	5.0	18.5	23.5
8	28.0	11.0	39.0	10.0	22.0	32.0	6.0	28.0	34.0
9	29.5	7.0	36.5	10.0	18.0	28.0	11.0	14.0	25.0
10	25.5	6.0	31.5	19.0	9.0	28.0	5.0	22.0	27.0
11	23.0	13.5	36.5	14.0	18.0	32.0	22.0	23.0	35.0
12	24.5	13.0	37.5	8.5	21.0	29.5	12.0	22.5	32.5
13	23.0	11.5	34.5	19.0	9.0	28.0	13.0	20.0	33.0
14	23.5	14.0	37.5	8.5	23.0	31.5	7.5	24.0	31.5
15	23.0	12.5	35.5	10.5	20.0	30.5	7.5	23.0	30.5

Table 8 (Continued)

Days	#310[a] Kafir	Peas	Total	#369 Kafir	Peas	Total	#376 Kafir	Peas	Total
16	24.5	11.5	35.5	20.0	9.0	29.0	7.0	20.0	27.0
17	24.0	11.0	35.0	9.5	23.0	32.5	4.0	27.5	31.5
18	24.5	12.5	37.0	11.0	19.0	30.0	7.0	19.0	26.0
19	19.0	15.0	34.0	16.0	22.0	38.0	6.0	22.0	28.0
20	22.5	16.0	38.5	9.0	20.0	29.0	5.0	23.0	28.0
21	22.5	16.0	38.5	10.5	19.5	30.0	9.0	23.0	32.0
22	16.0	13.0	29.0	12.0	10.0	22.0	4.0	23.0	27.0
23	17.0	14.0	31.0	9.0	15.0	24.0	7.0	23.0	30.0
24	15.5	18.0	33.5	9.0	20.0	29.0	5.0	22.0	27.0
25	14.0	22.0	36.0	15.0	11.0	26.0	3.0	23.0	26.0
26	18.0	21.0	39.0	7.0	21.0	28.0	3.0	24.0	27.0
27	23.0	14.0	37.0	8.0	20.0	28.0	3.0	25.0	28.0
28	18.0	18.0	36.0	11.0	9.0	20.0	5.0	21.0	26.0
29	18.0	16.5	34.5	8.0	19.0	27.0	7.0	24.0	31.0
30	15.0	20.0	35.0	7.5	19.0	26.5	10.0	20.0	30.0

<u>Note</u>.

a

Bird 310 was given kafir and peas. Birds 369 and 376 were given hemp, kafir, and peas but did not eat hemp.

ate kafir and peas in a very distinctive pattern. More kafir than peas was eaten on the intervening days during the first 16 and last 9 days of the observation period. More peas than kafir was eaten on days 17 through 21. The hypothesis that this pattern reflects a position bias is tested below.

Changes in the Number or Kinds of Seeds Ingested

While there were differences in the relative ingestion seen in the two, three and four grain presentations, all but three birds (306, 377, 526) ate varying amounts of the same kinds of seeds every day throughout the observation period. These three birds, which stopped or began eating a particular kind of seed, are of special interest. They show that the probability of a bird changing the kinds of seeds eaten under the present conditions is quite low, but that such changes may occur without experimental intervention.

It was thought that careful inspection of the data for these subjects (Tables 9 and 10) might reveal characteristic features which anteceded the changes in the kinds of seeds eaten. A knowledge of such features would permit the dissociation of non-experimentally and potential experimentally induced changes in seed ingestion. However, there were no readily apparent characteristics of these data for seed ingestion or of that for water intake or body weight

Table 9

Intake (g) of Corn, Kafir, Peas, and Vetch by Bird 306 on 30 Consecutive Days

Days	Corn	Kafir	Peas	Vetch	Total
1	4.5	15.0	6.0	7.0	32.5
2	6.0	15.5	2.5	4.0	28.0
3	11.0	14.0	2.0	6.0	33.0
4	9.5	4.0	10.5	7.0	30.0
5	6.0	9.0	8.0	2.5	25.5
6	9.0	13.0	4.0	4.0	30.0
7	10.0	13.5	3.0	7.0	33.5
8	11.0	6.0	1.5	7.5	26.0
9	9.5	8.0	7.0	4.0	28.5
10	13.5	7.0	8.0	3.5	32.0
11	12.0	6.0	11.0	3.0	32.0
12	15.0	3.5	4.0	4.0	26.5
13	14.0	4.5	7.5	6.5	32.5
14	9.0	5.5	5.5	6.5	26.5
15	20.0	4.5	6.0	5.5	36.0
16	17.0	2.0	0.0	6.0	25.0
17	9.0	5.5	1.0	12.5	28.0
18	9.0	6.0	3.5	9.0	27.5
19	13.0	9.0	5.5	16.0	43.5
20	6.5	0.0	0.0	8.5	15.0
21	11.0	8.0	1.5	15.5	36.0
22	8.0	7.0	2.0	10.0	27.0
23	9.5	6.0	3.5	11.0	30.0
24	9.5	6.0	1.0	13.0	29.5
25	13.5	8.0	3.0	13.0	37.5
26	9.5	7.0	0.0	9.5	26.0
27	10.5	6.5	0.0	9.5	26.5
28	10.5	6.0	0.0	9.0	25.5
29	9.5	6.0	0.0	9.5	25.0
30	9.0	8.0	0.0	10.0	27.0

Table 10

Hemp, Kafir, and Peas Intake(g) by Birds 377 and 526 on 30 Consecutive Days

	#377				#526			
Days	Hemp	Kafir	Peas	Total	Hemp	Kafir	Peas	Total
1	13.0	3.0	0.0	16.0	0.0	20.0	27.0	47.0
2	5.0	14.0	0.0	19.0	0.0	18.0	23.0	41.0
3	6.0	14.0	0.0	20.0	0.0	18.0	31.0	49.0
4	9.5	4.0	0.0	13.5	0.0	14.0	23.0	37.0
5	3.5	16.0	0.0	19.5	0.0	16.0	25.5	41.5
6	3.0	13.0	0.0	16.0	0.0	16.0	25.0	41.0
7	9.0	6.0	0.0	15.0	0.0	16.0	23.0	39.0
8	12.0	13.0	0.0	25.0	0.0	18.0	21.0	39.0
9	9.0	10.0	0.0	19.0	0.0	16.0	19.0	35.0
10	15.0	3.0	0.0	18.0	0.0	16.0	20.0	36.0
11	7.0	18.0	0.0	25.0	0.0	15.5	24.5	40.0
12	5.0	16.0	0.0	21.0	0.0	14.0	20.0	34.0
13	15.0	3.0	4.0	22.0	0.0	16.0	18.0	34.0
14	10.0	16.0	0.0	26.0	7.5	13.0	18.0	38.5
15	5.0	18.0	3.5	26.5	7.5	5.0	23.0	35.5

Table 10 (Continued)

Days	#377 Hemp	Kafir	Peas	Total	#526 Hemp	Kafir	Peas	Total
16	11.0	4.0	9.0	24.0	0.5	8.0	21.5	30.0
17	3.5	19.5	6.0	29.0	10.0	10.0	17.0	37.0
18	4.0	14.0	6.0	24.0	4.0	10.5	24.5	39.0
19	12.5	4.0	13.0	29.5	6.5	9.0	20.0	35.5
20	3.0	22.0	6.0	31.0	15.0	9.0	17.0	41.0
21	4.0	14.0	11.0	29.0	6.5	10.5	21.0	38.0
22	8.0	3.0	17.0	28.0	6.5	10.0	23.0	39.5
23	5.0	20.0	4.0	29.0	15.0	7.5	18.5	41.0
24	6.0	16.0	8.0	30.0	5.0	10.5	23.0	38.5
25	7.0	10.0	10.0	27.0	6.5	13.0	18.0	37.5
26	7.0	18.0	5.0	30.0	9.0	10.0	21.5	49.5
27	5.0	15.0	8.0	28.0	4.0	16.0	19.5	39.5
28	3.5	8.0	9.5	21.0	5.0	12.5	23.0	40.5
29	8.0	19.0	4.0	31.0	9.0	11.0	21.5	41.5
30	3.0	15.0	8.0	26.0	4.0	12.0	21.5	37.5

which predicted the subsequent changes in seed ingestion.

Position Biases and Differential Seed Ingestion

As indicated above, examination of the data for bird 369 suggested that this bird might have a position bias: peas were eaten in a greater amount than kafir on the days when the position of the seeds within the feeder was hemp, peas, kafir i.e., HPK, on days 1, 4, ... (See Section II); but not on other days when the position was PKH or KHP. While the position of each of the seeds was changed daily to prevent the development of position biases (Young, 1961; Irwin, 1971) it seemed that the great variability seen in the total daily food intake and/or the intake of each seed might be due to position biases. It also appeared that these biases might provide yet another measure of relative acceptability: some seeds might be eaten in large quantities in all positions while other seeds would be eaten only when they were placed in the most favored eating positions. Therefore, the data for seed ingestion were analyzed to determine the existence of two different kinds of position biases. First, birds could eat more food from one trough of the feeder than from another irrespective of the kinds of seeds in that trough. Over time, this position bias would tend to decrease the differences which might otherwise be found in the intake of seeds. Second, a bird could eat more from one of the feeding troughs only on those days when it contained a particular kind of seed.

None of the birds offered two grains showed position biases associated with kafir, peas or total food intake. Of the 19 birds fed three grains, only bird 507 showed position biases associated with the total food intake (Friedman Test; $p < .01$). This bird, which ate all three seeds but significantly less kafir than hemp or peas (See Table 6), also showed a position bias associated with kafir intake, but hemp and peas ingestion were not so affected. Eight other birds in this three grain group showed position biases associated with the ingestion of one or more seeds, as is seen in Table 11. Six of these eight birds ate only two of the three grains presented. Birds 393 and 394, which were fed four different kinds of seeds but ate only corn, kafir and vetch, showed position biases associated with the kafir intake.

Consideration of the above results and the results of the statistical analyses of the differential ingestion of seeds (Tables 5, 6, 7) indicated the degree of variability seen in the daily intake of the different kinds of seeds could not be attributed to position biases. The differential intake of seeds observed for birds given two, three or four grains was not related to differences in the location of the troughs but rather appeared to be associated with the characteristics of the different kinds of seeds presented.

Table 11

Kruskal-Wallis Analyses of Variance on Hemp, Kafir and Peas Intake(g) in Each Feeder Position During 30 Daily Three Grain Presentations

Bird Numbers	Grain	*H*	*p*
316	Hemp	3.5	ns
	Kafir	10.7	<.01
341	Hemp	0.6	ns
	Kafir	7.3	<.05
354	Hemp	7.9	<.02
	Kafir	4.8	ns
365	Hemp	11.6	<.01
	Kafir	17.2	<.001
369	Kafir	14.0	<.001
	Peas	18.5	<.001
377	Hemp	10.4	<.01
	Kafir	21.7	<.001
	Peas	1.2	ns
381	Hemp	10.4	<.01
	Kafir	13.0	<.01
	Peas	9.8	<.01
382	Hemp	7.0	<.05
	Kafir	1.7	ns
507	Hemp	5.1	ns
	Kafir	13.4	<.01
	Peas	6.4	ns

Note. K=3, df=2. Only birds with significant position biases associated with one or more seeds are shown.

Food and Water Intake and Body Weight

Analyses of variance indicated there were no differences in the mean daily food intake, water intake, or mean body weight for the groups presented two, three, or four grains (H=1.8, 5.1, and .3, respectively; df=2; ns, all cases). Coefficients of variation (Tables A-C) indicated that the variability in daily food and water intake and in body weight were similar to those of a previous report (Zeigler, et. al, 1972) which showed that variations in food and water intake were greater than variations in body weight. In the present study the variations in total food intake were slightly less (approximately 16%) than in the previous report (20% to 30%), wherein pigeons were fed "Columbia Special."

Tables D-F show several relationships between food and water intake and body weight. The birds drank from 1.5 to 6 times as much as they ate by weight. The water/food ratio averaged about 2.5. The water/body weight ratio showed a five-fold range, .05 to .25. With the possible exception of birds 20, 316 and 355, which ingested large amounts of hemp and showed relatively constant and similar water/food and water/body weight ratios; and of the birds given four grains, which showed similar water/food ratios, there was no apparent relationship between the differential ingestion of seeds (Tables 2, 3, and 4) and the interrelationships between food and water intake and body weight; the water/food, water/body weight and food/body weight ratios varied as much within the two, three and four-grain presentations as between them.

In contrast with the great intersubject variability seen in the water/food and water/body weight ratios, the food/body weight ratios were very similar for all birds. With one exception all birds ate 4%, 5%, or 6% of their body weight daily. The grand mean food/body weight ratio was .049 which agreed well with the value .047 reported for pigeons fed "Columbia Special" (Zeigler, et. al., 1972).

Discussion

Pigeons offered two, three or four different grains ad libitum for 30 days were highly individualistic in their ingestion of different grains and showed a highly variable ingestion of each kind of seed eaten. Despite this great variability in the daily intake of each seed, all but two birds showed a significantly different ingestion of the grains offered. However, because individual birds within groups showed significantly different but frequently opposite responses to the same grains, the two and four grain groups showed a similar ingestion of seeds. This presence of a significant differential ingestion of seeds by individual subjects but not by groups required statistical analyses of the seed ingestion of each bird.

A highly individualistic ingestion of seeds was also found in Brown's (1969) study of pigeons. What he called "an astonishing amount of individual variation" in the ingestion of different kinds of seeds was not related to differences in the size of the pigeon's bill nor to differences in feeding technique (contrast Kear's [1962] study of finches). These highly individualistic patterns suggest the presence of mechanisms which maintain differences between birds offered the same kinds of seeds. As the birds in Brown's study and the present subjects were mature when obtained from commercial lofts, it was not known whether the great individual differences observed were related to differences in the pigeon's previous developmental history or to anatomical, physiological or genetic differences between birds.

While all but three birds ate the same kinds of seeds during the 30-day observation period, there was a high degree of variability in the daily intake of seeds which exceeded the variability observed in the other measures recorded. Thus, it would appear that varying degrees of control subserve the maintenance of these several interrelated measures. The variability seen in the intake of each kind of food was greater than that seen for total food or water intake, and these measures were several times more variable than those for body weight.

Among a number of reasons for the great variability seen in the ingestion of individual seeds, several possibilities seem most cogent if one asks what kinds of environmental support would be required for the pigeon to ingest very constant amounts of each of several seeds each day. Reviews of the literature on seed predation (e.g., Janzen, 1971) and on the characteristics of seeds (Harper, Lovell & Moore, 1970) suggest that the periodic nature and geographic distribution of seed crops, and variations in seed characteristics within and between plant species, would not foster the evolution of mechanisms which could provide for the daily intake of constant amounts of different kinds of seeds. Given (1) the typically variable characteristics of seeds; (2) the fact that under field conditions pigeons also ingest stones, gravel, shells and other hard objects ("grit") which are used in the gizzard to crush seeds (Levi, 1963); and (3) the multitude of other factors which would typically affect feeding behavior (e.g., the presence of predators, the feeding of other avian species, etc.), the variability of the present data is not necessarily remarkable. In fact, studies of the crop contents of feral pigeons suggest that such factors do lead to a highly variable ingestion of foods (e.g., Murton, 1965).

The available information was not sufficient to determine whether the observed variability was intrinsic or was a problem of the pigeon's "capacity" (see Sidman, 1960).

However, the very significant differential ingestion of seeds and the stability observed in the kinds of seeds eaten during the 30-day observation period suggested that the proportions of different seeds eaten could be used as a primary dependent variable. The studies below provide additional information concerning the characteristics of this measure.

III B

Trans-situationality of the Differential Ingestion of Seeds

The variability (Brown, 1969) and nature of the data obtained in studies of seed ingestion may reflect factors other than a differential responsiveness to the stimulus characteristics of the seeds presented. For example, the differences in the results obtained in the two, three, and four grain presentations above (Section III A) were assumed to be related to the different numbers and kinds of seeds presented. Yet, it was possible that these differences reflected only a largely adventitious responding which would vary under different conditions of presentation. Therefore, an experiment was conducted to establish that the different proportions of seeds ingested in the two and three grain presentations did not merely reflect ungeneralizable responding dependent upon different methods of presenting seeds.

Two and three grain presentations were used with a single group of subjects divided into two subgroups. Each subgroup received these two treatments in a different sequence. The similarity of the seed ingestion of these subjects which received the same seeds under two different conditions of presentation indicated the degree to which the pigeon's differential ingestion of seeds was stable, predictable, and generalizable (Irwin, 1971).

Methods and Procedures

Subjects

Ten experimentally naive White Carneaux pigeons were randomly assigned to Groups 3GPG (N=4) and PG3G (N=6).

Procedures

The birds in Group 3GPG were given hemp, kafir, and peas *ad libitum* for 12 consecutive days. Then, during the next 12 days these same grains were presented in pairs, one pair per day, according to a predetermined, random sequence which was different for each bird. Thus, each of the pairs of grains was presented on four different days. The birds in Group PG3G received the paired grains during the first 12 days and then the three grain presentations. All other experimental conditions were as described in General Methods and Procedures.

Results

Inspection of the raw data indicated that the intake of each seed was generally greater in the paired presentations than in the three grain presentations apparently only because the total daily intake was taken from two sources instead of three sources in the former case. As the medians for daily intake could therefore not be used to compare the two presentations, analyses were computed on the total intake for each measure (Table 12). Mann-Whitney U Tests computed on these totals indicated that the hemp, kafir, peas, and total food intake was similar regardless of the order of presentation so the PG3G and 3GPG groups were combined. However, subsequent analyses indicated that the total intake of the combined groups was greater during the three grain presentations than during the paired presentations ($T=8$, $N=10$, $p < .05$). Therefore, percentages (Table 13) were used for the analyses of the intake of each kind of seed. Mann-Whitney U Tests confirmed that the PG3G and 3GPG groups ingested similar percentages of hemp, kafir, and peas in the paired and three grain presentations, so subsequent analyses were computed on the percentages for the combined groups. Wilcoxon tests indicated that peas intake was a greater percentage of the total intake in the three grain presentations than in the paired grain presentations ($T=6$, $N=10$, $p < .05$) and that the opposite (i.e., $3G < PG$) was true for kafir intake ($T=7$, $N=10$, $p < .05$). Hemp was a similar percentage of the total intake under both methods of presentation ($T=12$, $N=10$, ns).

The differential ingestion of seeds within each of the two methods of presentation was similar for five of

Table 12

Percent Hemp, Kafir, and Peas Ingested During 12 Days of Paired (PG) and Three Grain (3G) Presentations

Bird Numbers	Hemp		Kafir		Peas	
	PG	3G	PG	3G	PG	3G
Group 3GPG						
344	40.3	40.7	23.5	22.3	36.0	36.8
346	71.2	71.9	17.0	17.6	11.6	10.3
515	43.2	35.4	9.6	0.0	47.0	64.5
530	35.2	24.6	23.3	18.3	41.4	57.0
Group PG3G						
337	65.2	36.5	23.2	19.5	11.5	43.9
366	63.2	82.4	24.8	10.3	11.8	7.1
508	24.2	10.7	18.9	8.1	56.7	81.0
510	40.5	38.6	30.6	25.9	28.8	35.3
527	57.1	47.8	13.1	20.8	29.7	31.3
534	29.5	17.3	33.6	24.5	36.8	58.1

Table 13

Total Seed Ingestion (g) During 12 Days of Paired (PG) and Three Grain (3G) Presentations

Bird Numbers	Hemp		Kafir		Peas		Total Food	
	PG	3G	PG	3G	PG	3G	PG	3G
				Group 3GPG				
344	178.5	185.0	104.0	101.5	159.5	167.5	442.0	454.0
346	198.5	371.0	47.5	91.0	32.5	53.5	278.5	515.0
515	129.5	128.5	29.0	0.0	141.0	234.0	299.5	362.5
530	134.0	107.0	89.0	79.5	157.5	247.5	380.5	434.0
				Group PG3G				
377	291.5	169.0	104.0	90.5	51.5	203.5	447.0	463.0
366	289.5	326.5	114.0	41.0	54.5	28.5	458.0	396.0
508	92.0	41.5	72.0	31.5	215.5	312.0	379.5	385.0
510	195.5	202.0	147.5	135.5	139.0	184.5	482.0	522.0
527	222.0	179.5	51.0	81.5	115.5	115.0	388.5	376.0
534	101.5	68.0	115.5	96.0	126.5	227.5	343.5	391.5

the ten birds (Table 14). The differences observed in the seed ingestion of the other five birds reflected the differences in the peas and kafir intake in the paired and three grain presentations cited above.

Water Intake and Body Weight

There were no differences in the water intake or body weight of Group PG3G and 3GPG in the paired and three grain presentations ($U=16$, 17; $U=14$, 15; $N_1=4$, $N_2=6$, ns) nor for the combined groups ($T=16$, 20; $N=10$, ns) (Tables G and H).

Table 14

Differential Ingestion of Hemp, Kafir, and Peas in Paired (PG) and Three Grain (3G) Presentations

Bird Numbers	PG	3G
Group 3GPG		
344	H=P***>K	H=P**>K
346	H***>K***>P	H***>K*>P
515	P=H**>K	P*>H***>K
530	H***>K***>P	P***>H*>K
Group PG3G		
337	H***>K*>P	P=H***>K
366	H***>K=P	H***>K=P
508	P***>H=K	P***>H=K
510	H**>K=P	P=H=K
527	H**>P>K	H***>P***>K
534	P**>H=K	P***>K*>H

Note. Relationships shown are the results of Friedman and/or Wilcoxon tests. Equal signs indicate $p > .05$.

* $p < .05$

** $p < .02$

*** $p < .01$

Discussion

The two and three grain methods of presentation were very different. First, the daily intake of each seed was greater in the two grain presentations than in the three grain presentations probably because the total daily intake was distributed among fewer food sources in the former case. Second, it appears that a seed may be eaten in the two grain presentations even if it is not eaten in the three grain presentations (e.g., bird 515). This is not unexpected as pigeons offered a multiseed diet do not eat only one kind of seed (Personal Observation). However, even seeds eaten in small amounts when three grains are presented may be eaten in large amounts in the paired grain presentations. In the present case, kafir was a small percentage of the total intake in the three grain situation. When it was presented as the only alternative food to hemp or peas, on eight days in paired presentations, it was ingested in amounts larger than typical of the three grain situation. Thus, at the end of the 12 days of paired presentations, a greater percentage of kafir was eaten than in the 12 days of three grain presentations.

Although there were differences in the intake of kafir associated with changes in the method of presentation, the differential intake of five of the ten pigeons was the same in the paired and three grain presentations and the frequency of changes in the relationships between pairs of grains was not different from chance. The differential ingestion of seeds was no more variable under these different conditions of presentation than it was in Section III A above, wherein eight of 15 birds changed their differential ingestion between the first and second half of a 30 day period in which the same seeds were presented only by the three grain method.

These data suggest that the pigeons were responding to discriminanda associated with the seeds per se and not to discriminanda associated with the specific method of presentation (Irwin, 1971). Of course, the data do not show that seed ingestion is independent of the method of presentation (Ivlev, 1961). Probably half or most of these stocks of pigeons are fairly consistent in their differential ingestion of seeds. The remaining birds, seem more variable, and are likely to be so in many different situations. Thus, there is apparently no relationship between the method of presentation and changes in the differential ingestion of seeds.

III C

Effects of Restriction to a Least Eaten Seed

It has been suggested that experiences with a food during early developmental stages may affect a mature bird's subsequent response to that food. For example, Rabinowitch (1969) has suggested that Zebra Finches which experience the ingestion of a specific food during the fledging period subsequently ingest that food in ad libitum "choice" situations; and Goodwin and Hess (e.g., 1969) have suggested that chicks may become "imprinted" upon foods. Similar experiments conducted to assess the effects of prior ingestive experience during adult stages of development on the subsequent differential ingestion of mature birds have most frequently used foods which were either "novel" or mildly emetic (e.g., Kear, 1962; Brower, 1969).

In the present case, seeds are eaten in very different amounts by individual pigeons all of whom are maintained under similar conditions (Section II A; Brown, 1969). If relative novelty were the basis of the different levels of ingestion observed, then a short period of ingestive experience with only a least eaten seed might increase its subsequent ingestion. On the other hand, under conditions in which only a few different kinds of seeds are offered, a seed might be eaten in small amounts even if it contained very mildly noxious substances (See Cook, Atsatt & Simon, 1971). A period in which feeding was restricted to only this least eaten seed could increase the concentration of these substances and further decrease or prevent the subsequent intake of the least eaten seed.

An experiment was conducted to determine whether the kinds of seeds eaten in the smallest amount by each bird during one period would be ingested in increased or decreased quantities after a subsequent period of feeding on only that seed. Modification of the ingestion of seeds after this period of restricted feeding would: (1) suggest the plausibility of using "novelty" or "noxiousness" hypotheses to explain the differential ingestion of seeds; (2) provide another measure of the stability (resistance to modification) of the differential ingestion of seeds; and (3) suggest the possibility of modifying seed ingestion to "form" groups with the same differential ingestion of seeds for experimental purposes.

Methods and Procedures

Subjects

The subjects for this experiment were seven White Carneaux Pigeons. Birds 344, 515, and 530 had been offered hemp, kafir, and peas simultaneously and then in pairs in a 24-day period immediately prior to this experiment (See Group 3GPG, Section III B). The other four birds were experimentally naive.

Procedures

The seven birds were offered hemp, kafir, and peas *ad libitum* during a 12-day period; each bird was restricted to a diet of only the single seed that it had eaten in the smallest quantity during the first 12-day, prerestriction period. In a third 12-day, postrestriction period, hemp, kafir, and peas were again offered *ad libitum* to all seven birds. Data were collected and all other conditions were maintained as previously described.

Results

Seed Ingestion

The birds with previous experience eating hemp, kafir, and peas significantly changed their *ad libitum* intake of seeds after a period of restriction while the experimentally naive birds did not (Tables 15-17). Birds 344 and 515, experienced birds restricted to kafir, did not eat kafir after restriction and increased their hemp intake. Bird 530 with similar experience increased kafir intake and decreased peas intake. The experimentally naive birds also showed decreases (birds 327 and 511) and increases (bird 514) in the postrestriction intake of the seeds to

Table 15

Medians and Ranges for Seed Ingestion(g) During the Prerestriction, Restriction, and Postrestriction Periods by Experimentally Naive Birds

Bird Numbers	Seed[a]	Periods: Prerestriction Median	Prerestriction Range	Restriction[b] Median	Restriction[b] Range	Postrestriction Median	Postrestriction Range
511	H	9.3	2.0-13.5	28.5	25.0-32.0	6.3	1.0-18.0
	K	18.0	11.0-22.0			16.0	6.0-23.0
	P	12.3	5.0-16.5			12.5	9.0-17.5
	Total	38.0	23.0-42.0			36.3	26.5-45.0
514	H	3.5	1.0-14.5	24.8	20.0-29.0	8.3	3.0-11.5
	K	5.2	1.0-10.5			4.3	1.0- 7.0
	P	20.0	17.0-29.0			20.5	17.5-27.5
	Total	33.0	30.0-37.5			32.5	27.5-39.5
321	H	0.0		0.0		0.0	
	K	21.0	9.0-29.0			24.5	6.0-32.5
	P	18.5	10.5-31.0			17.5	10.5-25.0
	Total	38.0	30.0-50.0			38.5	26.5-48.0
327	H	14.3	8.5-20.0			16.8	9.5-31.5
	K	16.5	4.5-24.0	40.0	11.0-47.0	8.3	4.5-19.5
	P	25.8	14.5-34.0			28.0	12.5-38.0
	Total	54.8	41.0-63.0			53.0	43.0-66.0

[a] H=hemp, K=kafir, P=peas
[b] Only one kind of seed was offered during the restriction period.

Table 16

Medians and Ranges for Seed Ingestion(g) During the Prerestriction, Restriction, and Postrestriction Periods by Birds Previously Offered Hemp, Kafir and Peas

Bird Numbers	Seed[a]	Prerestriction Median	Prerestriction Range	Restriction[b] Median	Restriction[b] Range	Postrestriction Median	Postrestriction Range
344	H	12.0	6.0-20.0			15.8	12.0-21.5
	K	2.8	0.5- 4.0	32.5	24.0-40.5	0.0	
	P	23.0	18.0-26.0			18.5	11.0-32.0
	Total	38.3	28.5-47.5			35.8	25.0-53.0
530	H	12.0	4.5-15.5			11.8	6.5-15.5
	K	4.8	2.5- 7.5	29.3	20.5-31.5	6.8	5.0-12.0
	P	15.8	13.0-18.5			11.8	9.0-15.0
	Total	32.8	30.5-36.0			30.5	26.5-36.0
515	H	7.3	3.5-15.0			11.3	8.0-18.5
	K	5.2	0.5-13.5	19.0	9.0-28.5	0.0	
	P	16.0	3.5-22.0			18.0	11.5-25.5
	Total	28.5	18.5-32.5			30.5	21.5-44.5

[a]H=hemp, K=kafir, P=peas
[b]Only one kind of seed was offered during the restriction period.

Table 17

Mann-Whitney U Tests on the Pre- and Postrestriction Intake of Hemp, Kafir, and Peas

Bird Numbers	Seeds	*p*
Birds Previously Offered Hemp, Kafir, and Peas		
344	Hemp	$<.05$
	Kafir	$<.001$
	Peas	ns
530	Hemp	ns
	Kafir	$<.006$
	Peas	$<.001$
515	Hemp	$<.002$
	Kafir	$<.001$
	Peas	ns

Note. Mann-Whitney U Tests on the pre- and postrestriction ingestion of hemp, kafir, and peas by experimentally naive birds were not significant.

which they had been restricted (See Tables 15 and 16), but these changes were not significant. Bird 321 did not eat hemp in the prerestriction period or during or after restriction to hemp.

While only the experienced birds showed significant changes in the ingestion of individual seeds, all subjects (except bird 321) showed changes in the differential ingestion of seeds when the pre- and postrestriction periods are compared (Table 18). Thus, the postrestriction ingestion reflects significant (birds 344 and 515) and non-significant (birds 327 and 511) decreases as well as significant (bird 530) and non-significant (bird 514) increases in the restricted seed. Only bird 321, which was restricted to, but never ate hemp, showed no changes in seed ingestion. This bird, self-deprived during the restriction period, had sustained a body weight loss of 20% of its median *ad libitum* weight prior to the postrestriction period.

Total food intake was significantly less in the restriction period than in the prerestriction period ($T=0$, $N=7$, $p < .02$), but was similar in the restriction and postrestriction periods ($T=5.5$, $N=7$, ns; Table I).

Water Intake

There were no significant differences in water intake during the three observation periods for three of the seven

Table 18

Differential Ingestion of Seeds in the Pre- and Postrestriction Periods by Experimentally Naive Birds and Birds Previously Offered Hemp(H), Kafir(K), and Peas(P)

Bird Numbers	Restricted[a] Seed	Periods: Prerestriction	Periods: Postrestriction
		Experimentally Naive Birds	
511	Hemp(28.5)	$K \overset{*}{>} P \overset{**}{>} H$	$K=P \overset{*}{>} H$
514	Hemp(24.8)	$P \overset{**}{>} H=K$	$P \overset{**}{>} H \overset{*}{>} K$
321	Hemp(0)	K=P	K=P
327	Kafir(40.0)	$P \overset{**}{>} H=K$	$P \overset{*}{>} H \overset{*}{>} K$
		Birds Previously Offered Hemp, Kafir and Peas	
344	Kafir(32.5)	$P \overset{**}{>} H \overset{**}{>} K$	$P \overset{*}{>} H$
530	Kafir(29.3)	$P \overset{**}{>} H \overset{**}{>} K$	$H=P \overset{**}{>} K$
515	Kafir(19.0)	$P \overset{*}{>} H=K$	$P \overset{**}{>} H$

Note. The relationships indicated are the results of Wilcoxon Tests. Prior analyses of variance computed on the daily intake of seeds were significant in all cases ($p < .02$, or better for all cases except bird 511 postrestriction where $p < .05$).

[a]The numbers in parentheses are the median daily food intake(g) during the restriction period.

*$p < .05$

**$p < .01$

birds, and six of the seven birds had similar water intake in the pre- and postrestriction period (Tables I and J). Birds 321, 327, 530, and 515 showed decreases in water intake during the restriction period, which may be secondary to decreased food intake.

Body Weight

Birds 511 and 514 showed no changes in body weight over the three periods (Tables I and K). All other birds had a lower median body weight during the restriction period. Bird 327 regained this lost weight but other birds regained little--327, 344, and 515; or none, i.e., 321 and 530, of their lost body weight. Only bird 530 had a decreased postrestriction intake relative to the prerestriction period.

Discussion

The three birds used in a previous experiment in which hemp, kafir, and peas had been presented simultaneously and then in pairs (See Section III B) significantly changed their intake of the restricted seed in the postrestriction period. The four experimentally naive birds showed no significant change in the intake of any of the seeds when the pre- and postrestriction periods are compared. The subjects in both groups (except bird 321) showed changes in the differential ingestion of seeds associated with the (significant or non-significant) changes in the intake of the restricted seed. These changes were similar for the experienced and naive birds: some of the birds in each group decreased, and one bird in each group increased, the intake of the restricted seed. Thus, the primary difference between the experienced and naive groups was the significance of the differences between pre- and postrestriction intake of the restricted seed. The present experimental design does not show whether these differences in the response to restriction are due to the different feeding experiences, the length of time feeding on the three grains, or other factors.

The changes in seed ingestion did not clearly support either the novelty or "noxiousness" hypotheses. Restricting feeding to the least eaten seed did result in a subsequent decreased intake of this seed for two of the three birds which had previously eaten hemp, kafir, and peas. However, the other bird in this group increased the intake of the restricted seed in the postrestriction period. Because this sample is small, one cannot determine which experimental variables brought about these differences.

The changes observed in the differential ingestion of seeds could be due to such factors as (1) body weight loss during restriction; (2) nutrient imbalance; or (3) aversive postingestional factors. However, no single hypothesis would appear to account for the several different kinds of changes seen in the postrestriction period.

The body weight losses sustained by five of the seven birds during restriction do not appear to be the direct cause of changes in the differential ingestion of seeds. Bird 321, which sustained a 20% loss of body weight because it did not eat during the restriction period, was the only subject which showed no change in the differential ingestion of seeds. The responsiveness to different seeds may remain unchanged during periods when feeding does not occur. Caloric and nutrient depletion (and an absence of the possibility to associate these factors with specific food(s)) may differ from nutrient imbalance which becomes associated with feeding on one kind of seed. The possibility of an imbalance of nutrients is suggested by dietary experiments with rats which show that "selection" among foods of high nutrient value tends to be highly individualistic and unrelated to nutritional value. With the introduction of a single nutrient, which upsets the ratio of nutrients, there may be subsequent changes in food "selection" (Harper, 1967). Of course, it is not at present known whether and how rapidly pigeons respond to nutrient imbalance. Previous reports concerning the maintenance of pigeons on a diet of only kafir or only hemp remain equivocal (Levi, 1963). Nutrient imbalance or aversive postingestional effects would not appear to explain the increased median ingestion of the restricted seeds shown by birds 514 and 530.

The results show that the differential ingestion of seeds may be changed by non-surgical means. Further research is required to show the basis for these changes.

III D

The Effects of Food Deprivation on the Differential Ingestion of Seeds

The cyclicity of feeding in individuals and species reflects contingencies associated with the availability of food (Collier, Hirsch & Hamlin, 1972) and changes in responsiveness toward food which follow internally mediated changes in orogastric sensory structures (e.g., Wyrwicka, 1969). These sensory changes may increase the general responsiveness to foods, alter responsiveness to specific ingestants or change both. As general and specific responsiveness are dissociable, different mechanisms may serve them (Hinde, 1970). This suggests that different combinations of sensory structures serve general and specific responsiveness. For example, the pigeon's crop probably does not provide information about the specific nutritional qualities of its contents, but it does mediate a cyclicity of general responsiveness to food (Cardini, 1971).

While many investigators have suggested that specific responsiveness decreases with increasing body weight loss, or with the amount of time an animal is food deprived (e.g., Brown, 1969; Holling, 1965; Hinde, 1970), other investigators have suggested the opposite (Jacobs, 1967). These disparate views come from experiments with a variety of different species. However, opposing results may be obtained even when the same species is used because the relationships between general and specific responsiveness to foods vary with the method of controlling general responsiveness. The general responsiveness of pigeons and chickens may be increased by giving them larger than usual quantities or "piles" of food (Bayer, 1929; Brown, 1969). General responsiveness is also increased when these birds are exposed to cage-mates, or to machines which are "pecking" (Strobel & MacDonald, 1974), or when they are deprived of food to specified levels of body weight loss (e.g., Zeigler, et al., 1972). Pigeons given larger than usual quantities of food (50 vs. 25 grams of a 5-grain mixture) eat more but do not change the proportions of each kind of seed ingested (Brown, 1969). The effects of "pecking induction stimuli" from nearby birds, or from machines which model pecking, may "override the (peck) eliciting effects of shape, color, contrast...(and even the) ...learned associations between food stimuli and aversive effects (Strobel & MacDonald, 1974, p. 501), which would usually control the pecking of chicks. Thus, in Brown's study general responsiveness increased without changing specific responsiveness. Strobel and MacDonald increased general responsiveness concurrently with a tremendously decreased specific responsiveness.

The pigeon's general responsiveness to food has been described under both ad libitum and food deprived conditions. In this experiment the pigeon's specific responsiveness to seeds was observed after periods of food deprivation resulting in the same weight losses (10%, 20%, and 30%) used in previous studies of the pigeon's general responsiveness to food (See Zeigler, et al., 1974). The data from this experiment will be compared with similar data on the differential ingestion of seeds seen after body weight loss associated with surgical damage to the trigeminal "feeding system" (See Section IVA and IVB below).

Methods and Procedures

Subjects

The subjects for this experiment were six White Carneaux pigeons in Group PG3G described in Section IIIB above.

Procedure

A mean body weight was computed for each bird during a 12-day period in which hemp, kafir and peas were presented ad libitum. Each bird was then deprived of all food and weighed daily. When 10%, 20%, and 30% of its ad libitum weight had been lost, a bird was allowed to eat from its feeder box which contained 40 grams each of hemp, kafir, and peas at the beginning of each of several feeding periods. Seed ingestion was measured consecutively during three 5-minute periods, during three 15-minute periods, and then, during a single, uninterrupted 23-hour period. Each feeding period was terminated by removing the feeder box and was preceded by measures of seed ingestion, and the rotation of the seeds in the troughs. The measurement and rotation of seeds was conducted in the usual manner with one exception: these procedures were completed at the end of each feeding period instead of daily. All other experimental conditions were as described in Section II.

Results

1. Effects of Food Deprivation and Body Weight Loss on Total Intake in 5-Minute, 15-Minute, and 23-Hour Feeding Periods

Table 19 shows the total food intake of each bird in the 5-minute, 15-minute and 23-hour feeding periods at each level of body weight loss. The birds ate less food in successive 5-minute periods at all three levels of body weight loss (except bird 366 at 20%) and in successive 15-minute periods after a 10% weight loss (except bird 508). After losing 20% or 30% of their *ad libitum* weight, the tendency to decrease food intake was more variable but there was generally a decrease in seed ingestion during successive feeding periods of equal duration.

Total intake in the first 5-minutes of feeding was

Table 19

Total Food Intake (g) in Feeding Periods After 0%, 10%, 20% and 30% Body Weight Loss

Bird Numbers	Consecutive Feeding Periods 5m	5m	5m	5m	15m	15m	15m	1st hr Total	23 hrs	24 hrs
0% Body Weight Loss										
337										40.5
366										35.8
508										32.8
510										43.8
527										30.5
534										33.5
10% Body Weight Loss										
337	25.0	12.5	10.5	48.0	10.5	5.0	2.0	65.5	9.0	74.5
366	10.0	4.0	1.5	15.5	4.5	0.0	0.0	20.0	25.5	45.5
508	18.5	1.0	0.0	19.5	0.0	0.0	0.0	19.5	14.0	33.5
510	21.5	4.0	1.5	27.0	2.0	1.0	0.5	30.5	9.0	39.5
527	24.0	7.5	0.0	31.5	5.5	0.0	0.0	37.0	12.0	49.0
534	21.0	3.0	2.0	26.0	3.5	1.0	0.0	30.5	11.0	41.5
Total	120.0	32.0	15.5	167.5	26.0	7.0	2.5	203.0	80.5	283.5
20% Body Weight Loss										
337	25.5	12.5	11.5	49.5	2.0	2.5	8.0	72.0	18.5	90.5
366	6.5	10.0	3.0	19.5	14.0	0.0	0.0	33.5	13.5	47.0
508	42.0	5.5	1.5	49.0	0.0	0.0	0.0	49.0	5.5	54.5
510	20.0	10.0	4.0	34.0	4.0	3.0	0.0	41.0	18.0	59.0
527	27.5	16.5	11.5	55.5	7.0	6.5	0.0	69.0	4.5	73.5
534	19.5	16.0	5.5	41.0	9.5	3.0	4.0	57.5	20.5	78.0
Total	141.0	70.5	37.0	248.5	46.5	15.0	12.0	322.0	80.5	402.5

Table 19 (Continued)

Bird Numbers	Consecutive Feeding Periods 5m	5m	5m	5m	15m	15m	15m	1st hr Total	23 hrs	24 hrs
30% Body Weight Loss										
337	26.0	14.0	10.5	50.5	3.5	6.0	7.5	77.5	12.5	90.0
366	13.0	7.0	0.0	20.0	7.5	2.5	4.0	34.0	20.0	54.0
508	40.5	10.5	2.5	53.5	0.0	0.0	0.0	53.5	10.5	64.0
510	23.0	10.5	4.5	38.0	3.0	5.0	1.0	47.0	26.0	73.0
527	21.5	13.5	5.0	40.0	9.0	5.0	3.0	57.0	24.0	81.0
534	12.0	6.0	4.5	22.5	8.0	0.0	3.5	34.0	30.5	64.5
Total	136.0	61.5	27.0	224.5	41.0	18.5	19.0	303.0	123.5	426.5

65% or more of the total intake for the first hour of feeding for five of the six birds fed after a 10% weight loss. Greater losses of body weight led to the ingestion of greater amounts of food in the second and third 15-minute feeding periods. However, bird 508 ate more than half of its hourly intake in the first 5 minutes after sustaining a 20% or 30% body weight loss. Eighty-nine percent of this bird's diet in the first 5 minutes was large peas. While the total intake in the first 5 minutes for the grouped data was similar after the 10%, 20%, and 30% weight losses (Table 20), individual birds showed very different rates of food intake in the first 5 minutes, which in two cases were readily related to the kinds of seeds eaten (See Tables L-Q). The upper and lower extreme rates of food intake in the first 5 minutes were those of bird 508 (8.4g/m), which ingested large amounts of peas and was the first to terminate eating at all three levels of body weight loss; and of bird 366, which ate fewer peas than any of the other birds. The group's median rates of ingestion were 4.1 g/m after a 10% weight loss (ranges 2.0-4.8 g/m) and 4.5 g/m after weight losses of 20% and 30% (ranges 1.3-8.4 g/m; 2.6-8.4 g/m), respectively.

Total intake was significantly greater after weight losses of 20% and 30% than after a loss of only 10% in the second 5-minute feeding period but was similar for all three

Table 20

Friedman and Wilcoxon Tests on Group Total Food Intake (g) in Feeding Periods After 10%, 20%, and 30% Body Weight Loss

Feeding Periods	% Levels of Body Weight Loss Compared	p Friedman or Wilcoxon	Direction of Differences
1st 5m	10:20:30	ns	
2nd 5m	10:20:30	<.03	
	10:20	ns	
	20:30	ns	
	10: 30	<.05	10 < 30
3rd 5m	10:20:30	ns	
Sum of 5m periods	10:20:30	<.05	
	10:20	<.05	10 < 20
	20:30	ns	
	10: 30	ns	
1st 15m	10:20:30	<.05	
	10:20	<.05	10 < 20
	20:30	ns	
	10: 30	<.05	10 < 30
2nd 15m	10:20:30	ns	
3rd 15m	10:20:30	ns	
First Hour	10:20:30	<.005	
	10:20	<.05	10 < 20
	20:30	ns	
	10: 30	<.05	10 < 30
Next 23 Hours	10:20:30	ns	
24 Hours	10:20:30	<.006	
	10:20	<.05	10 < 20
	20:30	ns	
	10: 30	<.05	10 < 30
	0:10:20:30	<.01	
	0:10	ns	
	0: 20	<.05	0 < 20
	0: 30	<.05	0 < 30
	10:20	<.05	10 < 20
	10: 30	<.05	10 < 30
	20:30	ns	

levels of weight loss in the third 5-minute feeding period (Table 20).

The food eaten in the first three 5-minute periods, i.e., the first 15 minutes of feeding, illustrates the pigeon's ability to ingest large proportions of its daily intake in a relatively short period of time. As a group, the birds ate 82.5%, 77.0%, and 74% of their first hour's intake, and 59.0%, 62.0% and 53% of their total daily intake in the first 15 minutes after 10%, 20%, and 30% losses of body weight, respectively.

Total food intake in the first hour was significantly less after a 10% weight loss than after losses of 20% and 30%, but intake during the next 23 hours did not differ as a function of body weight loss.

2. Comparisons of the Median Daily *ad libitum* Food Intake and Total Daily (24-Hour) Food Intake After a 10%, 20%, and 30% Body Weight Loss

The median total daily food intake for the 12-day predeprivation period (0% Body Weight Loss, Tables L-Q) was significantly less than the total daily intake for each day of feeding after a 10%, 20%, and 30% loss of body weight and was less after a 10% loss of weight than after weight losses of 20% and 30%. Total daily intake was similar after body weight losses of 20% and 30%.

3. The Effects of Food Deprivation and 10%, 20%, and 30% Body Weight Loss on the Relative Ingestion of Hemp, Kafir, and Peas in 5-Minute, 15-Minute and 23-Hour Feeding Periods

Analyses of variance were computed on the percentages shown at the right of Tables L-Q because the total food intake increased with increasing body weight loss. When significant changes were found in the percentages of seeds eaten at different body weights, analyses were also computed using the respective grams shown at the left of each of these tables. This permitted one to determine whether there were both absolute and relative changes in seed ingestion. Analyses of variance indicated the percent intake of hemp, kafir, and peas did not vary as a function of body weight loss in any of the 5 or 15-minute periods nor in the combined 5-minute or 15-minute periods. However, analyses of the first hour's intake showed that relatively more hemp was eaten after a 30% weight loss than after a 10% loss while the opposite was true of peas ingestion (X_r^2=7.6 and 7.0, respectively; and K=3, N=6, $p < .03$, both cases; T=0, N=6, $p < .05$, both cases). The percent kafir intake did not change (X_r^2=4.3, K=3, N=6, ns). Statistical analyses computed on the grams intake in the first hour after 10%, 20%, and 30% losses of body weight showed that both hemp intake and total intake increased (X_r^2=9.3, K=3, N=6, p=.006, for each) but that the grams of kafir and peas eaten did not vary (X_r^2=.3 and 2.3; K=3, N=6, ns, both cases). Thus, in the first hour after a 30% body weight loss, hemp intake increased both absolutely and relatively when compared with the hemp eaten the first hour after a 10% weight loss. The grams of peas eaten remained the same and subsequently showed a relative decrease re the percentage of peas eaten after the 10% weight loss.

There were no differences in the percent hemp, kafir, and peas eaten at the different levels of body weight loss during the 23-hour or the 24-hour periods.

Inspection of Tables L-Q suggested that group analyses had combined many different patterns of seed ingestion. Therefore, a Friedman Analysis of Variance was computed to determine the effects of body weight loss on the intake of hemp, kafir and peas for each subject. The results of these analyses showed that the level of deprivation did not affect the percentages of any of the seeds eaten during the feeding periods. This suggested that the relative intake of each seed was constant at different levels of body weight loss and during the time periods represented.

4. Comparisons of the Median *ad libitum* Intake of Hemp, Kafir, and Peas With the *Intake of* these Seeds After a 10%, 20%, and 30% Body Weight Loss

A greater percentage of peas was eaten in the *ad libitum* condition than after each of the three levels of body weight loss (0%:10%:20%:30%; X_r^2=10.6, df=3, $p < .02$; 0%:10%, T=0, N=6, $p < .05$; 0%:20%, T=0, N=6, $p < .05$; 0%:30%, T=.5, N=6, $p < .05$). Peas intake was similar at each of the levels of body weight loss (10%:20%:30%, X_r^2=3.7, df=2, ns). An analysis of variance was computed on the grams of peas to determine whether there were changes in both absolute amounts and relative proportions ingested. The results showed that the grams of peas ingested per day after 0%, 10%, 20%, and 30% weight losses was similar (X_r^2=2.5, K=4, N=6, ns.) and that the decrease in peas ingestion was only a relative change.

Kafir intake was greater and kafir formed a greater percentage of the total daily intake after 20% and 30% losses of body weight than at the *ad libitum* weight (Percentage: X_r^2=10.6, K=4, N=6, $p < .02$; T=0, N=6, $p < .05$, comparisons stated; Grams: X_r^2=12.6, K=4, N=6, $p < .01$; T=0 N=6, $p < .05$, comparisons stated).

An analysis of variance computed on the percentage of hemp eaten daily at 0%, 10%, 20%, and 30% losses of body weight was not significant (X_r^2=6.2, K=4, N=6, ns) however there were significant changes in the grams of hemp ingested at different levels of body weight loss. Hemp ingestion was greater after body weight losses of 20% and 30% than in the *ad libitum* condition or after a 10% loss of body weight (T=0, N=6, $p < .05$; all comparisons stated). Hemp ingestion at 20% and 30% and at 0% and 10% levels of body weight loss was similar (T=2 and 1, respectively, N=6, ns, both cases).

Seed ingestion varied greatly among birds but was relatively constant for each bird at different body weights. It was possible that non-significant results were obtained in the analyses of variance because there was an interaction between the relative magnitude of seed ingestion and deprivation level, irrespective of the kind of seed. If this were true, one might expect food deprivation to increase the ingestion of those seeds which had been eaten in the largest amounts prior to deprivation and perhaps, to further decrease those eaten in the least amounts. On the other hand, deprivation could do the opposite, that is, could decrease the relative differences in the ingestion of different seeds. These two possibilities were tested. The first was tested by computing an analysis of variance on seed ingestion after each seed had been ranked according to the magnitude of the median percent ingestion for the predeprivation period. The seed a bird ate in the largest amount in the predeprivation period was assigned the rank 1, the least eaten seed was assigned the rank 3, etc. Then, the percentages for the seeds ranked 1 were tested as a function of deprivation level. This was also done for the second and third ranked seeds. The relative percent ingestion of the seeds ranked first, second, and third in the predeprivation period did not vary as a function of body weight loss (X_r^2=3.4, .8, and 6.6 for seeds ranked 1st, 2nd, and 3rd, respectively; K=4, N=6, ns, all cases).

For the second analysis, the percent ingestion of each of the seeds was ranked 1, 2, or 3 within each of the four levels of weight loss (0%, 10%, 20%, and 30%) for each subject. The largest percentages in each level of weight loss were analyzed together to determine whether the proportions of the groups' diet composed of the seed eaten in the largest quantity had changed as a function of weight loss. Analyses of variance were computed in the same manner for the 2nd, and 3rd ranked seeds.

The results indicated that the percentages, per se, did not change as a function of deprivation level (X_r^2=6.2, 1.8, and 3.1 for the percentages ranked 1, 2, and 3 respectively; K=4, N=6, ns, in all cases).

Water Intake

Water intake (Table R) decreased during food deprivation and increased on the days when food was presented. There was no significant difference in the amount of water ingested with the food eaten at the 0%, 10%, 20%, and 30% levels of weight loss (X_r^2=.2, K=4, df=3, N=6, ns).

Discussion

The percentages of hemp, peas, and kafir ingested during 24 hours was similar at the 10%, 20%, and 30% levels of body weight loss for both groups and individual birds. However, the percent intake of one or more seeds was significantly different from the median *ad libitum* percentage ingested at each of the three levels of weight loss. As the total food intake increased with each decrease in body weight, and as the grams of peas eaten did not change, the percentage of peas eaten decreased with increasing body weight loss. Thus, the percentage of peas eaten at each level of weight loss was significantly less than that eaten at the ad libitum body weight. The increase in the total daily food intake was primarily due to an increased ingestion of kafir and hemp which was significant at the 20% and 30% levels of weight loss. The percentage of peas eaten was thus decreased at 10%, 20%, and 30% of the ad libitum weight while the percent kafir ingestion increased at the 20% and 30% levels and the percent hemp ingestion increased at the 20% level relative to the percentages eaten at the ad libitum body weight.

There was no relationship between the rank order for the grams of each seed ingested before deprivation and the subsequent response to food deprivation. Thus, the results do not support the hypotheses that deprivation increases or decreases responsiveness to the "palatability" of foods. Unlike the previous preliminary results of Brown (1969) with three birds fed at 75% of their ad libitum body weight, the results did not suggest that deprivation diminishes differences in the percent ingestion of different kinds of seeds.

The data suggest that there may be a sequence in the intake of different kinds of seeds. Peas were generally eaten in the first 5 or 10 minutes of feeding by each animal. Not more than 2 grams of peas were eaten in the remaining 50 minutes of the first hour at any level of weight loss. Thus, the birds ate peas early in the first hour and then increasing amounts of kafir and hemp with increasing body weight loss. In almost all cases few or no peas were eaten during the last 23 hours of the day.

The results suggest that food deprivation does not change the pigeon's responsiveness to specific seeds but rather increases the probability that feeding will be continued. The additional feeding which occurs after deprivation results in an increased intake of the foods eaten at that time when feeding would typically cease. As the ingestion of additional seeds was not proportionate with the ingestion observed under *ad libitum* conditions, the proportions of seeds eaten during the 24 hour period after weight loss differed from that seen after a similar period of *ad libitum* feeding. The significance of these results are discussed below (Section IV A) in relation to the effects of body weight loss which follows trigeminal lesions.

IV. The Trigeminal Syndrome

Previous studies have shown that deafferentation of the trigeminal sensory branches or electrolytic lesions of afferent structures within the trigeminal feeding system of the pigeon produce a syndrome of feeding deficits whose severity is proportional to the number of (peripheral) trigeminal sensory branches sectioned or the bilaterality of the lesions produced in the (central) trigeminal structures (Zeigler, 1974a). The primary characteristics of the trigeminal syndrome are:

(1) An immediate postoperative aphagia and subsequent hypophagia manifested as a failure to compensate for weight loss by an increased food intake;

(2) A reduced general responsiveness to food manifested as a decreased frequency of consummatory responses;

(3) A reduced efficiency of feeding due to difficulty in propelling food from the beak tip toward the oral cavity (mandibulation) which increases the number of consummatory responses emitted per gram of small grains. The usual "sorting" of mixed grains may also be absent.

The similarity of the feeding deficits seen after lesions in the pigeon's trigeminal "feeding system" and the feeding deficits reported after lesions of the lateral hypothalamus of the rat, have led to suggestions that trigeminal damage may, in fact, underlie some of the characteristic deficits seen in the so-called lateral hypothalamic syndrome (Zeigler, Marwine & Karten, 1974). The lateral hypothalamic syndrome is characterized by a well-documented progressive partial recovery of feeding which is at first greatly dependent upon the gustatory qualities of the foods offered.

Lesions of the ventromedial hypothalamus in the rat have also been shown to lead to changes in responsiveness to the gustatory qualities of the rat's diet. Thus, evidence from studies of the ventromedial and lateral hypothalamus, and trigeminal lemniscus of the rat has shown a close association between the rat's general and specific responsiveness to foods. In each of these cases changes in total intake are concurrent with a "finickiness" or an enhanced responsiveness to the orosensory qualities of food.

The similarity of the lateral hypothalamic and trigeminal syndromes may suggest that the general and specific responsiveness of the pigeon would be altered as is the case in the rat. However, while gustatory quality appears to be of great significance for the feeding of the rat, the role of orosensory quality in the development and maintenance of orovisual associations underlying food selection in the pigeon are largely unexplored. There are presumably many potential sources of feedback in areas of the crop and upper digestive track, for example, which could mediate visual-visceral associations. On the other hand, personal observations of feeding birds suggest that foods which are spit out or tossed aside probably never move beyond the oral cavity. This would seem to preclude other than oral sources of feedback. In addition, there is a growing body of evidence which would lead one to predict that some food qualities would be more readily associated with visceral cues than others (e.g., Wilcoxon, Dragoin & Kral, 1971; Shettleworth, 1972).

Gustatory qualities would seem important. Pigeons do have taste buds, and respond well to the taste of fluids (Duncan, 1960). However, their ingestion of grit, pebbles mixed with dirt, and of seeds, which may be dusty, would suggest that other or additional orosensory cues may be used. The trigeminal orotactile sense subserved by the pigeon's trigeminal sensory nerves and by the trigeminal "feeding system" may provide a basis for orovisual associations which underlie the pigeon's specific responsiveness to foods as manifested in the relative ingestion of different kinds of seeds.

Two experiments were designed to test the hypothesis that trigeminal damage alters the specific responsiveness to foods. The first study (IV A) compares the seed ingestion of pigeons before and after they sustained surgical procedures for peripheral deafferentation of the ophthalmic and mandibular branches of the trigeminal nerve. The second study (IV B) compares seed ingestion before and after electrolytic lesions of higher order neurons within the trigeminal "feeding system."

IV A

Effects of Two-Branch Trigeminal Lesions on the Differential Ingestion of Seeds

If the peripheral trigeminal branches provide a sensory basis for orovisual associations which are presumed to be necessary for the significant and individualistic differential ingestion of seeds observed above (Section III A), then surgical damage to these branches, which provide orotactile sensitivity, should alter the seed ingestion as observed prior to surgery.

Methods and Procedures

Subjects

The subjects were 15 experimentally naive adult male and female White Carneaux pigeons adjusted to the laboratory and then maintained on a feeding regimen as described above in General Methods and Procedures. They were randomly assigned to four groups offered different kinds of seeds. One group of two birds was offered corn, hemp, peas and vetch; one group of four birds was offered corn, kafir, peas and vetch; another group of four birds was offered hemp, kafir and peas; and five birds were offered only kafir and peas. These groups are designated CHPV, CKPV, HKP AND KP, respectively.

General Procedure

The subjects were maintained on the feeding regimen for at least 30 days during which food and water intake and body weight were measured as described previously. Then, two birds which had been offered hemp, kafir and peas were anesthetized only. All other birds were subjected to surgical procedures for bilateral deafferentation of the ophthalmic and mandibular branches of the trigeminal nerve. Subsequent to anesthetization or surgery all birds were maintained on the same seeds and feeding regimen as before treatment, for at least 30 days. Food, water and body weight were measured in the usual manner.

Surgical Procedures

From one to three birds were deafferented on each of several days. The birds were deprived of food from 4:30 p.m. the day before surgery until immediately after the surgery which was conducted before 4:30 p.m. the following day. Each bird was anesthetized with Equithesin (2.0 m./kg). Then, the feathers were cut from its head and from the sides of the lower beak and the subject's head was placed within a specially designed holder.

Ophthalmic sections. A midline incision was made in the scalp which was then drawn laterally to allow orbital access. A small incision was made in the skin along the curve of the orbital bone, this skin was drawn laterally and the eyeball was gently depressed to permit microscopic examination of the roof of the orbital cavity. The ophthalmic branch was gently teased ventrally at a point of passage beneath the superior oblique muscle and a section was cut, removed, and measured. The orbital skin was replaced, the procedure was repeated on the opposite side and the midline incision was closed with surgical wound clips. Then the surgical procedures for sectioning the mandibular branch were begun.

Mandibular sections. An incision was made in the skin on the side of the lower beak exposing the mandibular branch which lies within a small recess on the surface of the mandible a few mm from the point where the upper and lower beaks meet to within a few mm from the beak tip. The mandibular branch was cut free of rootlets within the recess, the proximal and distal ends of the nerve were cut and a section of the nerve was removed and measured. In a few cases small rootlets prevented the removal of an intact section of the nerve and in these cases the length of the small recess was gently scraped to remove and/or damage any remaining portions of the nerve. This procedure was repeated on the opposite mandible and the bird was returned to its cage where food and water were available *ad libitum*.

Results

Preoperative Seed Ingestion

The statistical analyses reported in the experiment above indicated that the pre- and postoperative seed ingestion was quite variable and that there were long term changes in the intake of different kinds of seeds within the preoperative period. To clarify the kinds of changes occurring within the preoperative period and facilitate the dissociation of potential surgically induced changes in seed ingestion from the long term presurgical changes observed, statistical analyses were computed on all measures recorded in the first and second 15 preoperative days, period 1 and period 2, respectively. The data from periods 1 and 2 were compared with that from the first and second 15 postoperative days, period 3 and period 4. As most birds did not begin eating immediately after surgery, the first day of period 3 was defined as the first postoperative day on which a bird ate at least 50% of its mean total food intake for period 2. The data and statistical analyses for the pre- and postoperative seed ingestion are presented below. To clarify the method of presentation, the criteria for determining the success of the surgical intervention are discussed first.

Surgical Results

Histological techniques have not been developed yet to assess the relative completeness of ophthalmic and mandibular deafferentation. However, previous research has shown that the effects of trigeminal deafferentation on the postoperative recovery of food intake and body weight is approximately proportional to the number of trigeminal branches sectioned (Zeigler, 1974a). Thus, the extent of deafferentation was determined indirectly for the animals in the present experiment by comparing their postoperative recovery of food intake and body weight (Table 21) with the criteria established for different degrees of deafferentation shown in Table 22.

Birds which were aphagic for three days, or which were aphagic for two days and below their mean (period 2) body weight more than 19 days, were assumed to have received complete bilateral two-branch lesions. Those with only one day of aphagia and which took ten or more days to recover their body weight were assumed to have received complete bilateral deafferentation of only one of the two trigeminal branches. Bird 377 was never aphagic and therefore was considered a surgical control.

The criterion for body weight was not used if a bird lost weight prior to surgery and then sustained additional weight loss. Inspection of the means and

Table 21

Extent of Trigeminal Deafferentation as Determined by Postoperative Food Intake, Body Weight Loss, and Body Weight Recovery

Group[a]	Bird Numbers	Extent[b] of Deafferentation	Days of Aphagia	Number of Days Below 50% of Mean Period 2 Food Intake	Number of Postsurgical Days Below Period 2 Body Weight[c]
CHPV	400	2BR	2	0	33*
	399	1BR	1	0	11
CKPV	393	2BR	3	1	44*
	306	2BR	3	0	21*
	394	2BR	2	0	36*
	392	IN	1	2	37*
HKP	341	2BR	3	1	27*
	377	SC	0	1	6
	507	A	0	0	5
	526	A	0	0	1
KP	395	2BR	3	0	15*
	405	2BR	2	1	23*
	413	1BR	1	2	19
	310	1BR	1	0	11
	398	1BR	1	2	10

[a]C=corn, H=hemp, K=kafir, P=peas, V=vetch.
[b]1BR=one branch, 2BR=two branch, IN=indeterminate (see text), SC=surgical control, A=anesthetized only.
[c]Data were collected the number of postsurgical days indicated by asterisks; 30 days for birds 377, 399, 507 and 526; 29 days for birds 413 and 310; 27 days for bird 398.

Table 22

Effects of Trigeminal Deafferentation Upon Food Intake and Body Weight Loss and Recovery

Group	N	Days of Aphagia		Percent Body Weight Loss		Number of Days Below *ad libitum* Body Weight	
		Mean	SD	Mean	SD	Mean	SD
Control	8	0.4	0.4	3.1	1.1	3.9	2.3
Ophthalmic	2	(2,2)	-	(7,9)	-	(10,17)	-
Mandibular	2	(2,1)	-	(8,6)	-	(17,14)	-
Ophthalmic & Mandibular	8	2.9	0.8	8.9	1.1	24.0	9.7

Note. Adapted from Zeigler (1974b).

statistical analyses on body weight (Tables S-U) indicated that birds 310, 392, and 393 weighed less in period 2 than in period 1. However, birds 310 and 393 were assigned to the one- and two-branch lesion groups, respectively, on the basis of their postoperative recovery of body weight and/or their number of aphagic days. While bird 392 was aphagic the same number of days as bird 310, it was not assigned to a lesion group because of its markedly reduced presurgical weight and continued weight loss (Tables S and T) and is designated "indeterminate."

For these considerations, seven subjects have been designated two-branch birds, four subjects have been designated one-branch birds, one bird is a surgical control, and another bird is indeterminate (See Table 21).

Effects of Deafferentation on Seed Ingestion

The medians and ranges for seed ingestion, means and standard deviations for total food intake and the results of statistical analyses on seed ingestion are shown in Tables 23-25. Tables 26 and 27 give the results of these analyses in summary form.

The effects of deafferentation were most frequently manifested as (1) changes in the kinds of seeds eaten and/or (2) immediate changes in the relative rank ingestion of seeds. A few deafferented birds showed (3) an immediate decrease in the grams difference between

Table 23

Medians and Ranges for Seed Ingestion(g) in 15 Day Periods Before Trigeminal Deafferentation

Group	Bird Numbers	Extent[a] of Deafferentation	Seed[b]	PRE Period 1 Median	PRE Period 1 Range	PRE Period 2 Median	PRE Period 2 Range
CHPV	400	2BR	H	21.3	17.0-28.5	19.3	14.5-21.5
			V	5.0	1.0- 8.5	3.5	1.5- 6.0
			Total	27.2	21.0-36.5	22.5	17.5-25.0
	399	1BR	C	8.8	0.5-12.0	10.3	8.0-14.5
			H	17.5	13.5-23.0	20.3	17.5-25.5
			V	0.8	0.0- 5.0	1.3	0.0-10.5
			Total	28.3	20.5-35.0	33.8	30.0-43.0
CKPV	393	2BR	C	10.5	4.5-15.0	10.8	5.0-16.0
			K	11.8	8.0-14.0	9.3	7.5-11.0
			V	7.8	5.5-17.0	6.7	4.5-11.5
			Total	30.3	23.0-38.5	25.3	21.5-36.5
	306	2BR	C	9.3	3.5-13.5	2.8	0.0- 3.5
			K	7.3	6.0-11.5	13.8	7.0-18.5
			V	10.3	8.5-13.0	11.3	7.5-19.5
			Total	27.0	18.0-37.5	28.4	22.5-37.5
	394	2BR	C	9.8	5.0-16.0	10.3	8.0-15.0
			K	7.5	4.0- 9.0	6.3	3.5- 8.0

Table 23 (Continued)

Group	Bird Numbers	Extent[a] of Deafferentation	Seed[b]	PRE Period 1 Median	PRE Period 1 Range	PRE Period 2 Median	PRE Period 2 Range
CKPV	394	2BR	P	0.0		0.0	
			V	13.5	11.0-17.0	14.3	11.0-19.0
			Total	29.8	26.0-37.0	31.0	23.5-36.5
	392	IN	K	12.0	9.0-21.5	10.3	7.5-12.5
			V	15.1	10.0-20.5	8.5	4.0-14.0
			Total	15.3	10.0-20.5	9.0	4.0-14.0
HKP	341	2BR	H	10.0	4.0-19.5	13.0	5.5-20.0
			K	19.0	5.0-25.5	20.0	4.0-26.0
			Total	28.3	23.0-33.5	27.7	21.0-42.5
	377	SC	H	5.3	3.0-12.5	7.9	3.0-15.0
			K	15.0	3.0-22.0	13.8	2.0-21.0
			P	8.3	0.0-17.0	11.0	4.0-19.0
			Total	28.3	21.0-31.0	30.7	26.0-38.0
	507	A	H	12.3	9.0-24.5	12.0	7.0-16.5
			K	7.8	2.0-19.5	8.8	3.5-13.5
			P	16.5	9.0-23.0	12.5	6.0-17.0
			Total	37.5	32.0-51.5	33.6	26.5-36.5
HKP	526	A	H	0.0	0.0- 7.5	6.4	0.5-15.0
			K	16.3	14.0-20.0	10.2	7.5-16.0
			P	22.9	18.0-31.0	21.1	17.0-24.5
			Total	38.8	34.0-49.0	39.0	30.0-41.5

Table 23 (Continued)

Group	Bird Numbers	Extent[a] of Deafferentation	Seed[b]	PRE			
				Period 1		Period 2	
				Median	Range	Median	Range
KP	395	2BR	K	9.7	6.0-13.0	12.1	9.0-13.0
			P	16.0	12.0-27.5	9.0	6.0-12.5
			Total	26.0	19.0-34.5	20.7	18.5-23.5
	405	2BR	K	5.8	1.5- 9.0	7.8	5.0-10.0
			P	24.0	22.0-26.0	18.8	17.0-25.0
			Total	30.3	23.5-33.0	27.0	24.5-31.5
	413	1BR	K	35.5	27.0-40.0	35.3	32.5-38.0
			P	0.0	0.0- 6.0	0.0	--
			Total	36.5	33.0-40.0	36.3	32.5-38.0
	310	1BR	K	23.3	16.0-29.5	17.5	13.0-23.0
			P	12.8	6.0-16.0	17.3	10.0-22.0
			Total	35.8	29.0-38.5	35.0	23.5-39.0
	398	1BR	K	14.5	9.0-16.0	14.5	12.0-18.0
			P	13.8	2.0-19.0	16.8	12.5-21.0
			Total	28.0	13.0-34.0	31.3	24.5-36.0

[a] 1BR=one branch, 2BR=two branch, IN=indeterminate (see text); SC=surgical control; A=anesthetized only.
[b] C=corn; H=hemp; K=kafir; P=peas; V=vetch

Table 24

Medians and Ranges for Seed Ingestion(g) in 15 Day Periods After Trigeminal Deafferentation

Group	Bird Numbers	Extent of Deafferentation[b]	Seed[c]	POST Period 3 Median	POST Period 3 Range	POST Period 4 Median	POST Period 4 Range
CHPV	400	2BR	H	15.0	10.0-19.0	13.5	9.5-17.0
			V	7.3	4.5-14.0	9.3	5.0-12.5
			Total	22.5	16.0-29.0	22.3	19.5-28.5
	399	1BR	C	8.8	5.0-12.0	10.5	5.0-15.0
			H	19.0	12.0-23.0	19.8	16.0-24.0
			V	3.3	0.0- 9.0	0.9	0.0- 5.0
			Total	32.8	19.5-39.5	31.8	26.5-35.5
CKPV	393	2BR	C	15.3	8.0-18.0	16.3	12.0-18.0
			K	0.0		0.0	
			V	12.8	8.0-15.0	8.0	4.0- 9.5
			Total	27.8	17.5-31.0	24.0	19.5-26.5
	306	2BR	C	0.2	0.0- 3.5	0.0	
			K	15.8	13.0-22.0	15.5	11.0-16.0
			V	13.3	5.0-16.0	12.5	5.0-15.0
			Total	30.0	18.0-38.0	28.3	16.0-30.5
	394	2BR	C	9.0	2.0-14.0	7.5	3.5-12.0
			K	10.3	2.5-14.5	8.3	6.0-14.5

Table 24 (Continued)

Group	Bird Numbers	Extent of Deafferentation[b]	Seed[c]	POST Period 3 Median	POST Period 3 Range	POST Period 4 Median	POST Period 4 Range
CKPV	394	2BR	P	0.4	0.0-11.5	7.0	0.0-18.0
			V	9.7	3.5-13.0	4.3	1.0- 7.5
			Total	31.3	23.5-34.5	27.3	19.5-31.5
	392	IN	K	12.3	0.0-16.0	10.5	4.0-13.0
			V	10.8	6.0-18.0	7.3	1.0-10.0
			Total	22.5	18.0-26.0	16.8	13.0-21.0
HKP	341	2BR	H	18.3	6.0-25.0	18.3	11.5-21.5
			K	10.0	0.0-21.0	11.2	8.5-14.5
			Total	26.0	11.5-37.5	29.5	22.5-32.5
	377	SC	H	13.5	1.0-24.0	6.8	0.0-11.0
			K	6.0	0.0-19.5	4.8	0.0-14.0
			P	17.0	0.0-24.0	22.7	11.0-25.0
			Total	30.0	25.0-44.0	33.4	19.0-35.5
	507	A	H	8.8	6.0-11.5	5.8	4.0-13.0
			K	12.3	7.0-19.0	15.1	10.5-20.0
			P	8.8	5.5-13.5	4.3	0.0-10.0
			Total	30.2	24.0-38.0	29.0	20.5-33.0
	526	A	H	3.8	1.0-8.5	3.8	2.0- 8.5
			K	12.0	8.5-19.0	12.8	8.0-18.0
			P	18.5	12.5-25.5	19.5	13.0-26.5
			Total	35.0	27.5-43.0	35.5	28.5-45.0

Table 24 (Continued)

Group	Bird Numbers	Extent of Deafferentation[b]	Seed[c]	POST Period 3 Median	Period 3 Range	Period 4 Median	Period 4 Range
KP	395[a]	2BR	K	8.8	5.0-14.0	-	-
			P	12.0	3.0-19.5	-	-
			Total	19.0	12.0-29.0	-	-
	405	2BR	K	0.0	0.0- 0.5	0.0	-
			P	26.1	16.0-31.0	26.0	21.5-28.5
			Total	26.1	16.0-31.0	26.0	21.5-28.5
	413	1BR	K	22.0	13.5-27.0	18.8	15.5-22.0
			P	10.3	6.0-20.5	17.5	11.0-26.0
			Total	32.0	22.0-42.5	34.8	31.5-43.5
	310	1BR	K	2.3	0.0- 8.5	0.0	-
			P	34.5	16.5-38.5	34.9	31.5-38.0
			Total	37.5	21.0-44.0	35.0	32.0-38.0
	398	1BR	K	6.7	0.0-12.5	2.0	0.0- 4.0
			P	27.5	21.0-35.5	29.5	25.0-32.5
			Total	34.8	24.0-48.0	30.0	27.0-35.5

[a]There are no data for period 4.
[b]1BR=one branch, 2BR=two branch, IN=indeterminate (see text), SC=surgical control, A=anesthetized only.
[c]C=corn, H=hemp, K=kafir, P=peas, V=vetch

Table 25

Mann-Whitney U Tests on Seed Ingestion in 15 Day Periods Before and After Trigeminal Deafferentation

Group[a]	Bird Numbers	Extent of Deafferentation[c]	Seed	Direction of Differences					
				1vs.2	2vs.3	3vs.4	1vs.3	2vs.4	1vs.4
CHPV	400	2BR	H	1>2**	2>3**	3=4	1>3**	2>4***	1>4***
			V	1=2	2<3***	3=4	1<3*	2<4***	1<4**
			Total	1>2**	2=3	-	1>3*	-	1>4**
	399	1BR	C	-	-	-	-	-	-
			H	-	-	-	-	-	-
			V	-	-	-	-	-	-
			Total	1<2***	2=3	-	1<3**	-	1<4*
CKPV	393	2BR	C	1=2	2<3**	3=4	1<3**	2<4***	1<4***
			K	1>2***	2>3***	3=4	1>3***	2>4***	1>4***
			V	1>2*	2<3***	3>4	1<3***	2<4*	1=4
			Total	1>2**	2=3	3>4	1=3	2>4*	1>4**
	306	2BR	C	1>2***	2>3**	3=4	1>3***	2>4**	1>4***
			K	1<2***	2<3*	-	1<3***	-	1<4**
			V	-	-	-	-	-	-
			Total	-	-	-	-	-	-
	394	2BR	C	-	-	3=4	-	2>4***	1>4**
			K	1=2	2>3***	3=4	1<3***	2<4***	1<4*
			P	1=2	2<3*	3<4*	1<3*	2<4***	1<4***
			V	1=2	2<3***	3>4***	1>3***	2>4***	1>4***
			Total	-	-	3>4**	-	2>4**	1>4**

Table 25 (Continued)

Group[a]	Bird Numbers	Extent of Deafferentation[c]	Seed	Direction of Differences					
				1vs.2	2vs.3	3vs.4	1vs.3	2vs.4	1vs.4
CKPV	392	IN	K	1>2**	2=3	-	1=3	-	1>4**
			V	1>2***	2=3	3>4**	1>3	2=4	1>4***
			Total	1>2***	2<3**	3>4***	1<3**	2=4	1<4***
HKP	341	2BR	H	-	-	3=4	-	2<4**	1<4**
			K	1=2	2>3**	3=4	1>3**	2=4	1>4*
			Total	-	-	-	-	-	-
	377	SC	H	-	-	-	-	-	1=4
			K	-	-	3=4	-	2>4**	1>4**
			P	-	-	3<4**	-	2>4***	1<4***
			Total	1<2**	2=3	-	1<3**	-	1<4**
	507	A	H	1=2	2>3**	3=4	1>3***	2>4**	1>4***
			K	1=2	2<3**	3<4*	1<3**	2<4***	1<4***
			P	1>2**	2>3**	3>4**	1>3***	2>4***	1>4***
			Total	1>2**	2>3*	-	1>3***	-	1>4***
	526	A	H	1<2***	2>3**	3=4	1<3***	2>4**	1<4**
			K	1>2***	2<3*	3=4	1>3*	2<4**	1>4*
			P	1=2	2=3	-	1>3**	-	1>4**
			Total	1=2	2>3*	-	1>3*	-	1=4
KP	395[b]	2BR	K	1<2**	2>3***		1=3		
			P	1>2***	2=3		1>3**		
			Total	1>2***	2=3		1>3**		

Table 25 (Continued)

Group[a]	Bird Numbers	Extent of Deafferentation[c]	Seed	Direction of Differences					
				1vs.2	2 vs.3	3vs.4	1vs.3	2vs.4	1vs.4
KP	405	2BR	K	1<2**	2>3***	3=4	1>3***	2>4***	1>4***
			P	1>2***	2<3***	3=4	1<3**	2<4**	1=4
			Total	1>2**	2=3	-	1>3**	-	1>4**
	413	1BR	K	1=2	2>3***	3>4*	1>3***	2>4***	1>4***
			P	1=2	2<3***	3<4**	1<3***	2<4***	1<4***
			Total	-	-	-	-	-	-
	310	1BR	K	1>2***	2>3***	3>4**	1>3***	2>4***	1>4***
			P	1<2***	2<3***	3=4	1<3***	2<4***	1<4***
			Total	-	-	-	-	-	-
	398	1BR	K	1=2	2>3***	3>4***	1>3***	2>4***	1>4***
			P	1<2*	2<3***	3=4	1<3***	2<4***	1<4***
			Total	1<2*	2=3	-	1<3**	-	1<4*

Note. Prior analyses of variance computed on the daily intake of each kind of seed and on total intake (1:2:3:4; 1:2:3; and 2:3:4) were significant ($p < .02$, or better, with the exception of 2:3:4 for H and K, bird 341 and K, birds 377 and 526 where $p < .05$) unless indicated (-).

[a]C=corn, H=hemp, K=kafir, P=peas, V=vetch.

[b]There were no data for period 4.

[c]1BR=one branch, 2BR=two branch, IN=indeterminate (see text), SC=surgical control, A=anesthetized only.

Table 26

Kinds of Seeds Eaten in 15 Day Periods Before and After Trigeminal Deafferentation

Group[a]	Bird Numbers	Extent[c] of Deafferentation	PRE		POST	
			Period 1	Period 2	Period 3	Period 4
CHPV	400	2BR	HV	HV	HV	HV
	399	1BR	CHV	CHV	CHV	CHV
CKPV	393	2BR	CKV	CKV	CV	CV
	306	2BR	CKV	CKV	CKV	KV
	394	2BR	CKV	CKV	CKPV	CKPV
	392	IN	KV	KV	KV	KV
HKP	341	2BR	HK	HK	HK	HK
	377	SC	HKP	HKP	HKP	HKP
	507	A	HKP	HKP	HKP	HKP
	526	A	HKP	HKP	HKP	HKP
KP	395[b]	2BR	KP	KP	KP	--
	405	2BR	KP	KP	P	P
	413	1BR	KP	K	KP	KP
	310	1BR	KP	KP	KP	P
	398	1BR	KP	KP	KP	KP

[a] C=corn, H=hemp, K=kafir, P=peas, V=vetch.
[b] There are no data for period 4.
[c] 1BR=one branch, 2BR=two branch, IN=indeterminate (see text), SC=surgical control, A=anesthetized only.

Table 27

Differential Ingestion of Seeds in 15-Day Periods Before and After Trigeminal Deafferentation

Group[a]	Bird Numbers	Extent[c] of Deafferentation	PRE Period 1	PRE Period 2	POST Period 3	POST Period 4
CHPV	400	2BR	H>V	H>V	H>V	H>V
	399	1BR	H>C>V	H>C>V	H>C>V	H>C>V
CKPV	393	2BR	K>V=C	K=C>V	C>V	C>V
	306	2 BR	V>C=K	K>V>C	K>V>C	K>V
	394	2BR	V>C>K	V>C>K	C=K=V>P	C>V[d]
	392	IN	K=V	K=V	K=V	K=V
HKP	341	2BR	H=K	H=K	H=K	H>K
	377	SC	K>H=P	H=K=P	H=K=P	H=K=P
	507	A	H=P>K	H=K=P	K>H=P	K>H=P
	526	A	P>K>H	P>K>H	P>K>H	P>K>H
KP	395[b]	2BR	P>K	K>P	K=P	-
	405	2BR	P>K	P>K	P>K	P>K
	413	1BR	K>P	K (only)	K>P	K=P
	310	1BR	K>P	K=P	P>K	P>K
	398	1BR	K=P	P>K	P>K	P>K

Note. Relationships shown are results of Friedman and/or Wilcoxon tests. Equal signs indicate p>.05.

a C=corn, H=hemp, K=kafir, P=peas, V=vetch

b There are no data for period 4.

c 1BR=one branch, 2BR=two branch, IN=indeterminate (see text), SC=surgical control, A=anesthetized, only.

d All other pairs equal.

the intake of two or more seeds; i.e., seeds were ingested in equal or more nearly equal amounts.

Since the medians for seed ingestion (Tables 23 and 24) cannot reveal the temporal characteristics of postoperative changes in seed ingestion, and thus do not show the basis for the dissociation of more immediate, surgically induced changes from long term changes in preoperative seed ingestion, daily data are also presented (See Figures 3-13 below). The daily data for all periods are presented in graphic form for 11 subjects. Graphs of daily data are not presented for certain birds for the following reasons: birds 341 and 377 showed significant position biases; bird 392 was defined as indeterminate; and bird 399 did not show any changes in the relative ingestion of different kinds of seeds. The daily data for these birds are presented in Tables V-Y.

The results are discussed below, by group, in terms of each bird's changes in the kinds of seeds eaten and/or changes in the differential ingestion of seeds. All but one subject showed significant changes in the ingestion of seeds within the preoperative period. Therefore, these changes are cited only where they are relevant for an understanding of an apparent surgical effect.

Group CHPV

Changes in the Kinds of Seeds Eaten. Birds 399 and 400, which sustained one- and two-branch lesions, respectively, ingested the same kinds of seeds in all four periods (Table 26).

Changes in the Differential Ingestion of Seeds. Bird 399 which sustained the one-branch lesion, showed no significant changes in seed ingestion in any period but bird 400, which sustained sections of both trigeminal branches ate significantly more vetch and less hemp after surgery (Table 25). Thus, the magnitude of the grams difference between the intake of hemp and vetch was significantly greater in the preoperative periods than it was after the two-branch sections (See Figure 3).

Group CKPV

Changes in the Kinds of Seeds Eaten. Birds 306, 393, and 394, which received two-branch lesions each ate different kinds of seeds after surgery (Table 26). Bird 306 (Figure 4) stopped eating corn in period 3, but as this subject decreased corn intake before surgery the postoperative changes in corn intake cannot be attributed to deafferentation. Bird 393 (Figure 5) ate at least 7.5 grams of kafir on each preoperative day but did not eat kafir in postoperative periods 3 and 4. Bird 394 (Figure 6) showed a different kind of change than birds 392 and

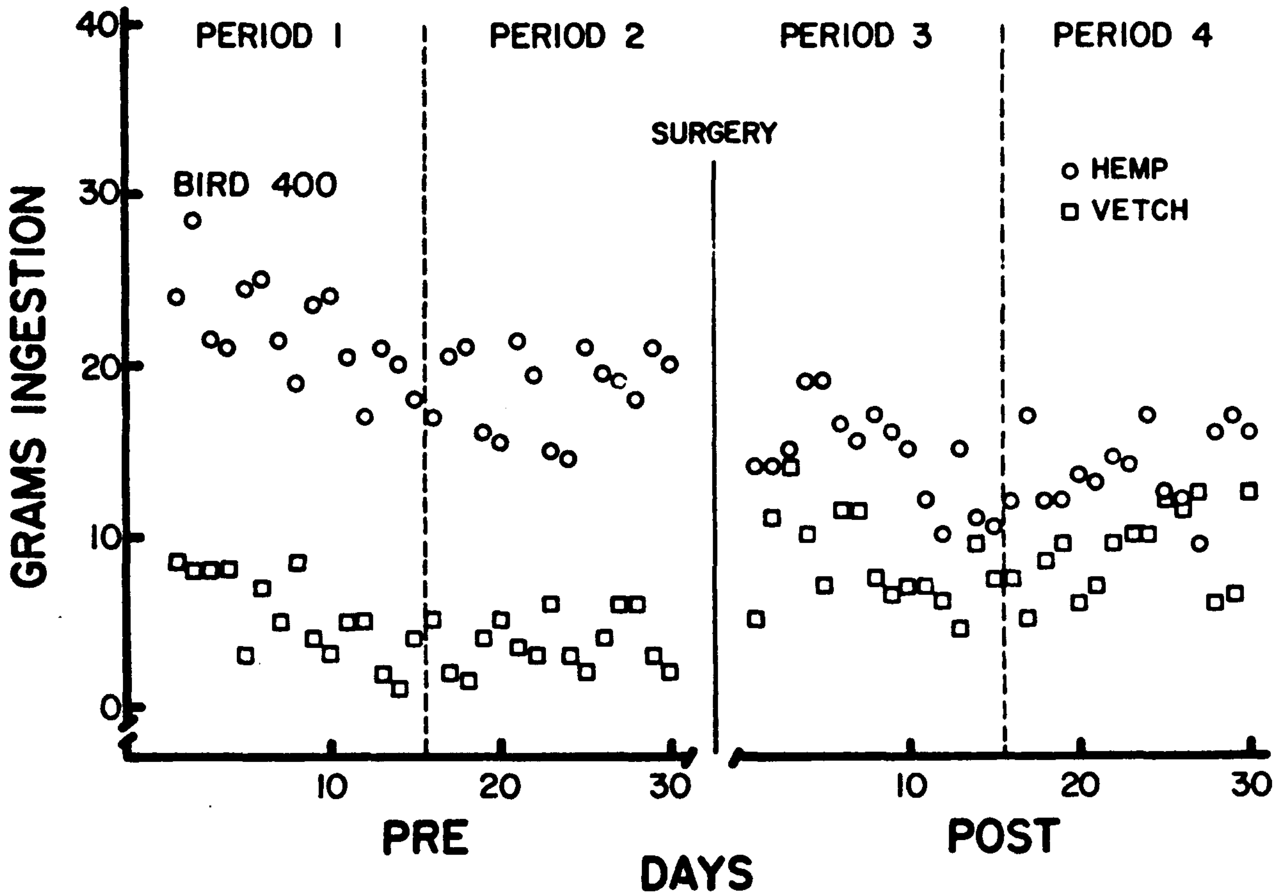


FIG. 3. Seed ingestion(g) by bird 400 pre- and postoperatively. Corn, hemp, peas, and vetch were offered ad libitum during 4 consecutive 15-day periods. Corn and peas were not eaten. This bird sustained a two-branch trigeminal lesion.

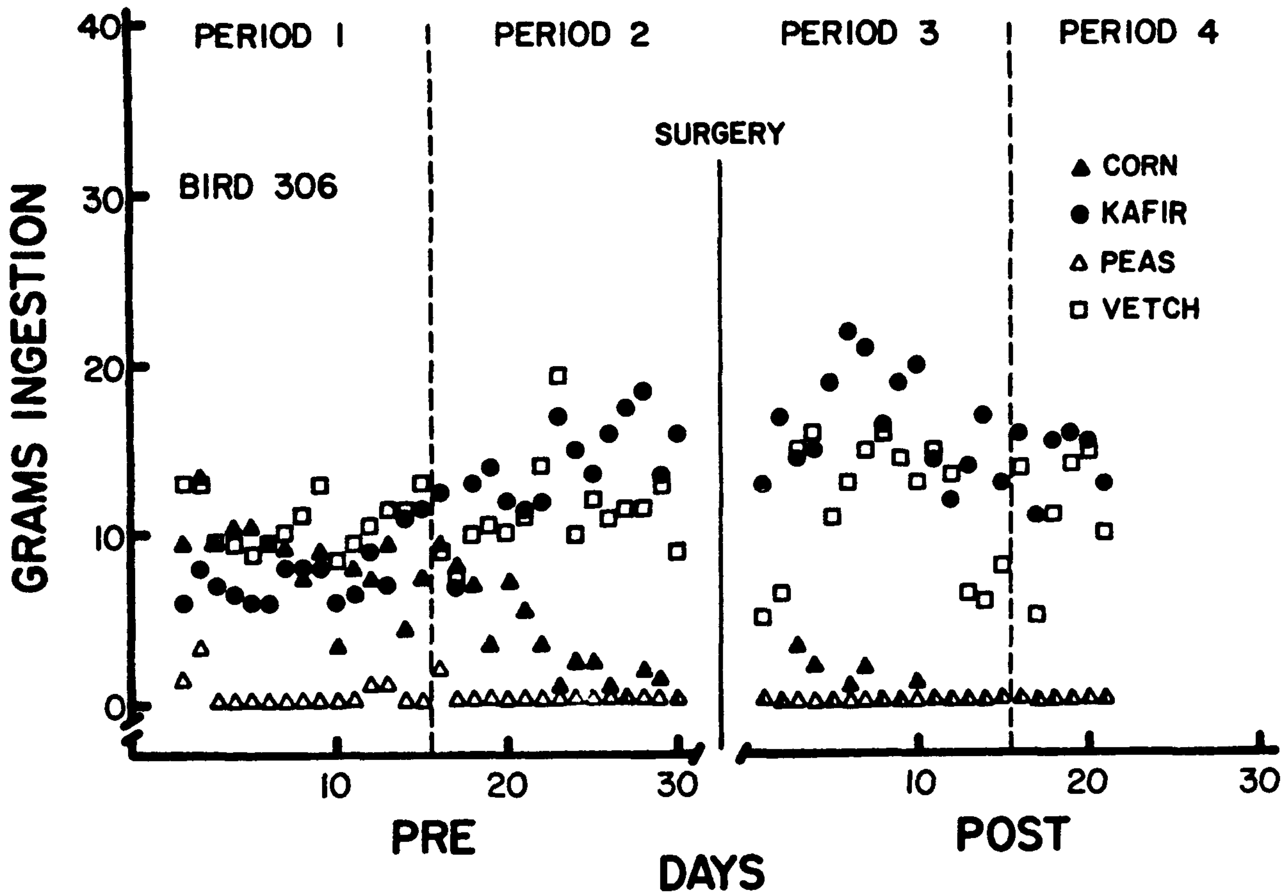


FIG. 4. Seed ingestion(g) by bird 306 pre- and postoperatively. Corn, kafir, peas, and vetch were offered <u>ad libitum</u>. Periods 1, 2, and 3 were 15 days each. Period 4 was 6 days. This bird sustained a two-branch trigeminal lesion.

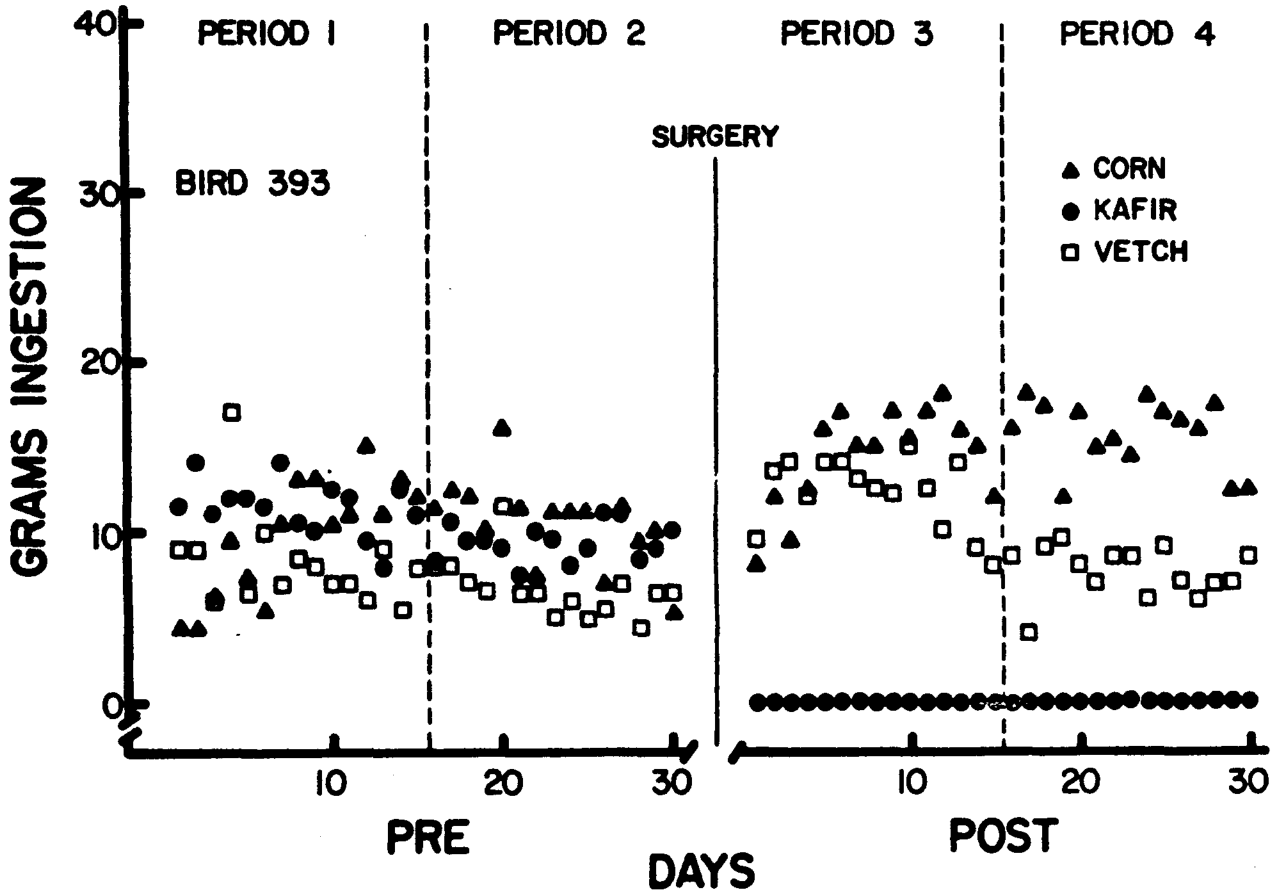


FIG. 5. Seed ingestion(g) by bird 393 pre- and postoperatively. Corn, kafir, peas, and vetch were offered ad libitum during 4 consecutive 15-day periods. Peas were not eaten. This bird sustained a two-branch trigeminal lesion.

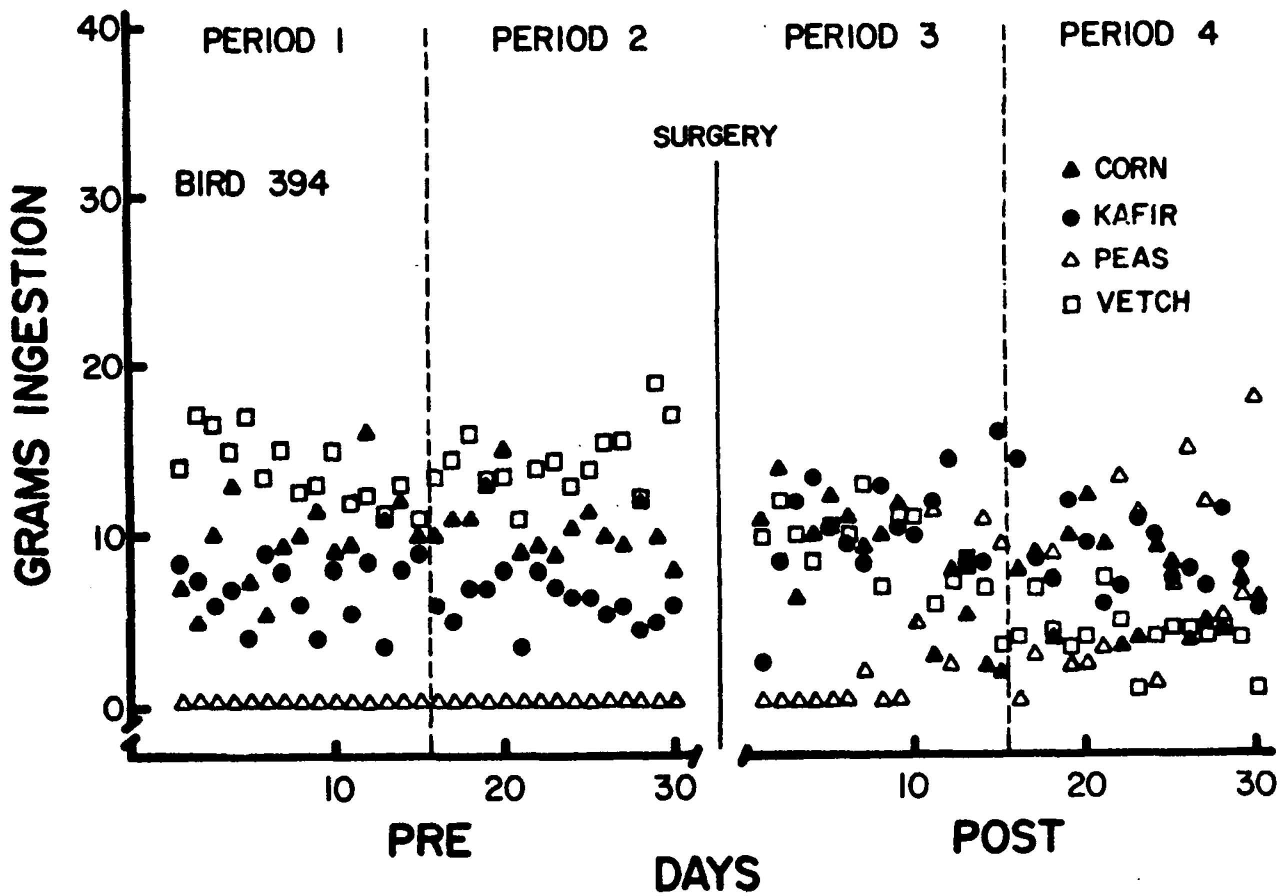


FIG. 6. Seed ingestion(g) by bird 394 pre- and postoperatively. Corn, kafir, peas, and vetch were offered ad libitum during 4 consecutive 15-day periods. This bird sustained a two-branch trigeminal lesion.

393: it began ingesting peas which were previously not eaten.

Changes in the Differential Ingestion of Seeds. The differential ingestion of seeds changed in the post-operative periods for animals which received two-branch lesions. Birds 306 and 393, which stopped eating one of the kinds of seeds eaten in period 2, showed significant, compensatory increases in the ingestion of those seeds which continued to be eaten (Figures 4 and 5), but showed no other changes in seed ingestion. Bird 394 (Figure 6) ingested significantly different amounts of corn, kafir, and vetch in preoperative periods 1 and 2. After surgery this subject ingested similar amounts of these seeds in period 3 and also began, and then increased, the intake of peas which were previously not eaten. Peas ingestion equalled that of the other grains in period 4. There were no changes in the differential ingestion of seeds shown by bird 392, the subject whose preoperative weight loss prevented assignment to a surgical group.

Group HKP

Changes in the Kinds of Seeds Eaten. All subjects in this group ate the same kinds of seeds in all four periods.

Changes in the Differential Ingestion of Seeds. Birds 507 and 526, which were only anesthetized, showed no immediate changes in seed ingestion comparable to the changes seen for birds subjected to the surgical procedures for two-branch lesions (Figures 7 and 8). These (anesthetized) subjects did show significant long-term increases in kafir intake and decreases in hemp intake within the four periods as is shown in Tables 24 and 25. The changes shown are opposite those seen for birds 341 and 377 which were assigned two-branch and surgical control lesions, respectively. The birds sustaining surgical procedures decreased their median kafir intake and increased their median hemp intake (Table 24), however, statistical analyses indicated these changes were not significant (Table 25) due to position biases (see Section III A). These biases led to an extensive overlap of the values for the daily grams intake of hemp and kafir. Thus, while the pre- and postoperative median intake of hemp and vetch seen in Table 24 are very different, the ranges shown overlap extensively in both the pre- and postoperative periods.

Group KP

Changes in the Kinds of Seeds Eaten. Bird 413 ate peas only on the first two preoperative days and after sustaining a one-branch lesion. All other subjects ate both kafir and peas in all four periods.

Changes in the Differential Ingestion of Seeds. While only one of the subjects fed kafir and peas changed the kinds of seeds eaten (Table 26), all subjects

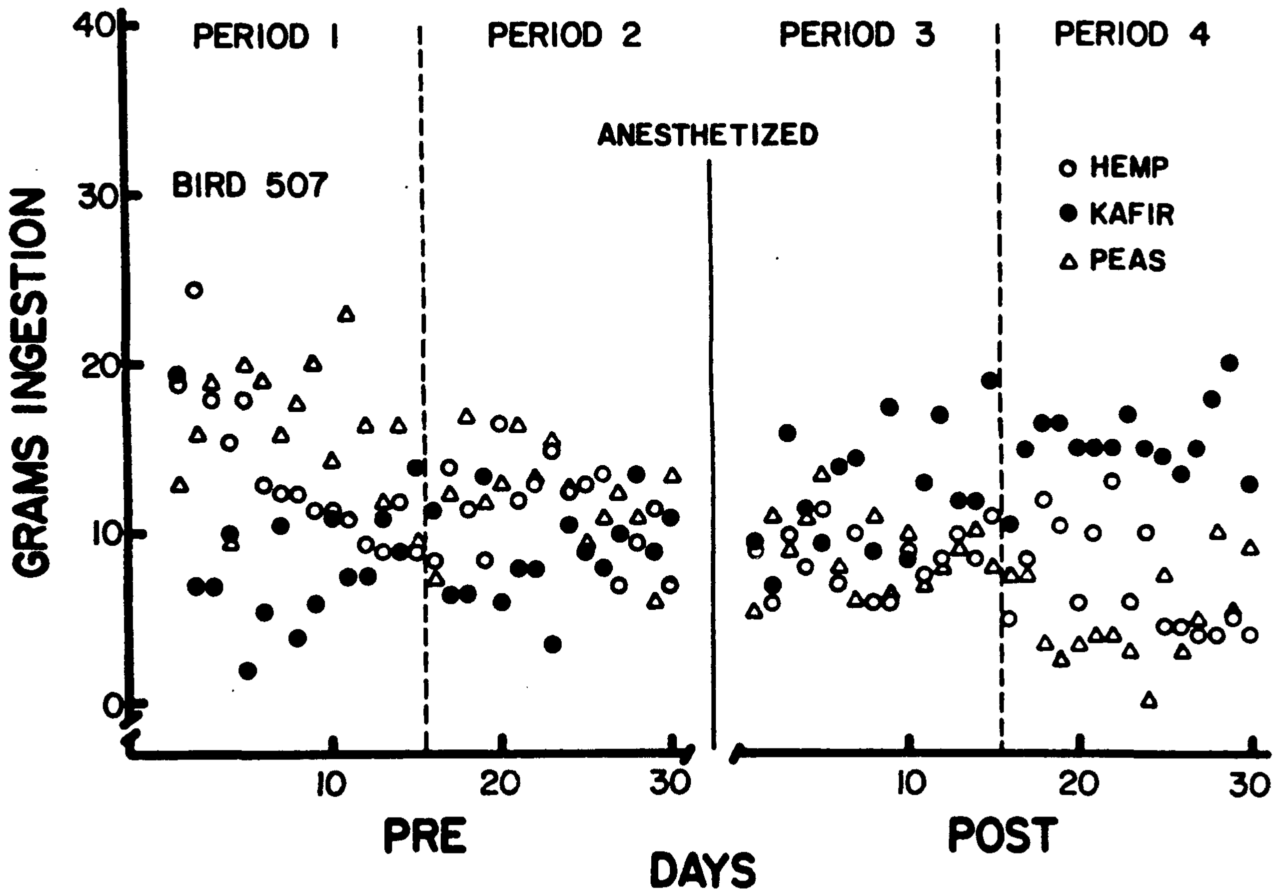


FIG. 7. Seed ingestion(g) by bird 507. Hemp, kafir and peas were offered <u>ad libitum</u> during 4 consecutive 15-day periods. This bird was anesthetized, only.

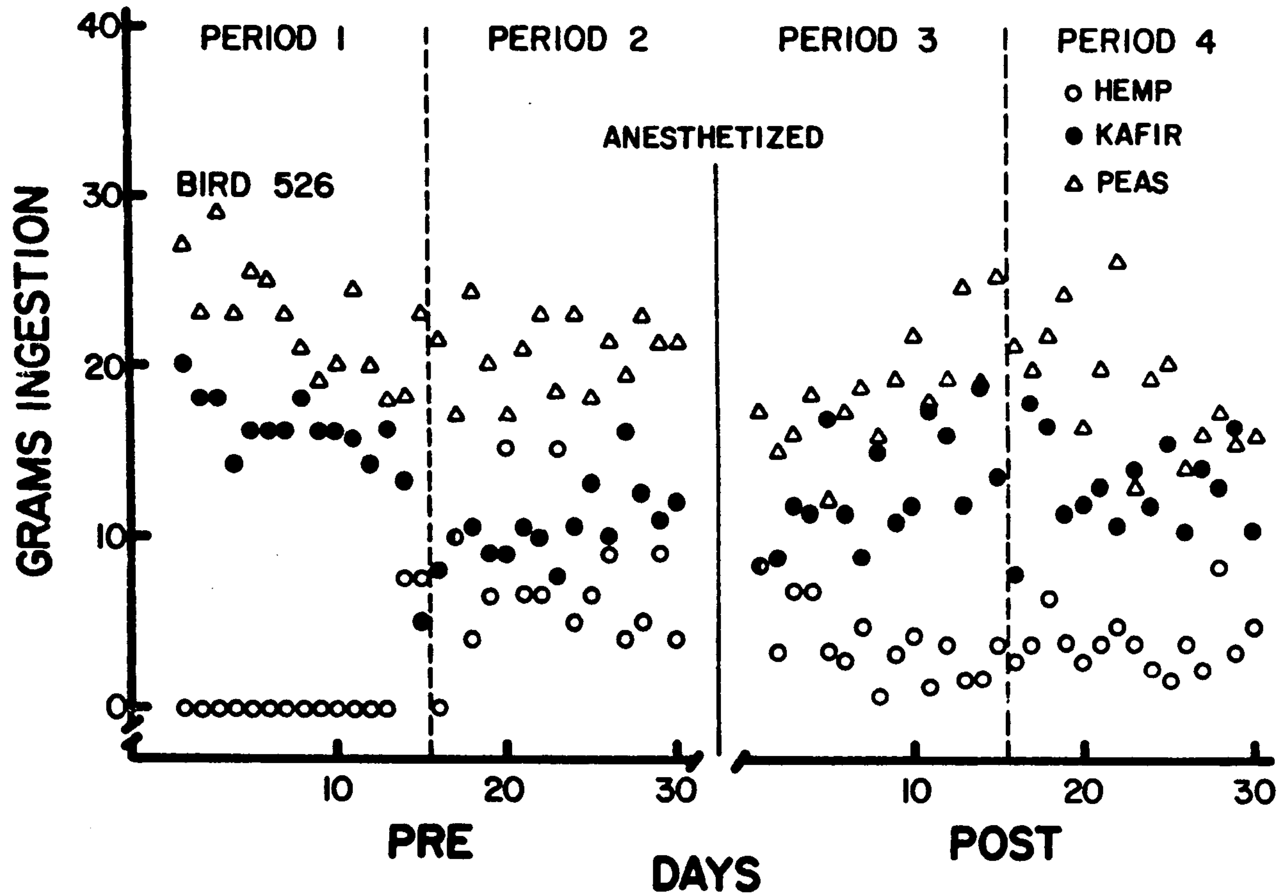


FIG. 8. Seed ingestion(g) by bird 526. Hemp, kafir and peas were offered ad libitum during 4 consecutive 15-day periods. This bird was anesthetized, only.

showed significant postoperative decreases in kafir intake, and with the exception of bird 395, significant increases in peas intake (Table 25). Inspection of the daily data for these subjects (Figures 9-13) shows that four of the five birds increased their peas ingestion by the second day of period 3, despite the facts that: (1) there was a wide range of preoperative levels of peas ingestion (e.g., birds 405 and 413) and (2) some birds increased, and other birds decreased, peas intake between periods 1 and 2 (Tables 24 and 25). While all subjects decreased kafir intake in the third period, the form of this decline varied greatly; intake decreased to zero for three birds (310, 398, and 405) after 1 to 20 days, but never fell below 5 grams for bird 395, nor below 13.5 grams for bird 413 (Figures 10 and 13). Both birds with one-branch lesions and birds with two-branch lesions changed their hemp and kafir intake. The specific form of the immediate postoperative changes of birds with one- and two-branch lesions were not readily dissociable on the basis of (1) the number of aphagic days; (2) the number of days required to regain *ad libitum* body weight; or (3) the magnitude of postoperative changes in seed ingestion.

Effects of Deafferentation on Total Food Intake

The means and standard deviations and the results of statistical analyses on total food intake (Tables 23,

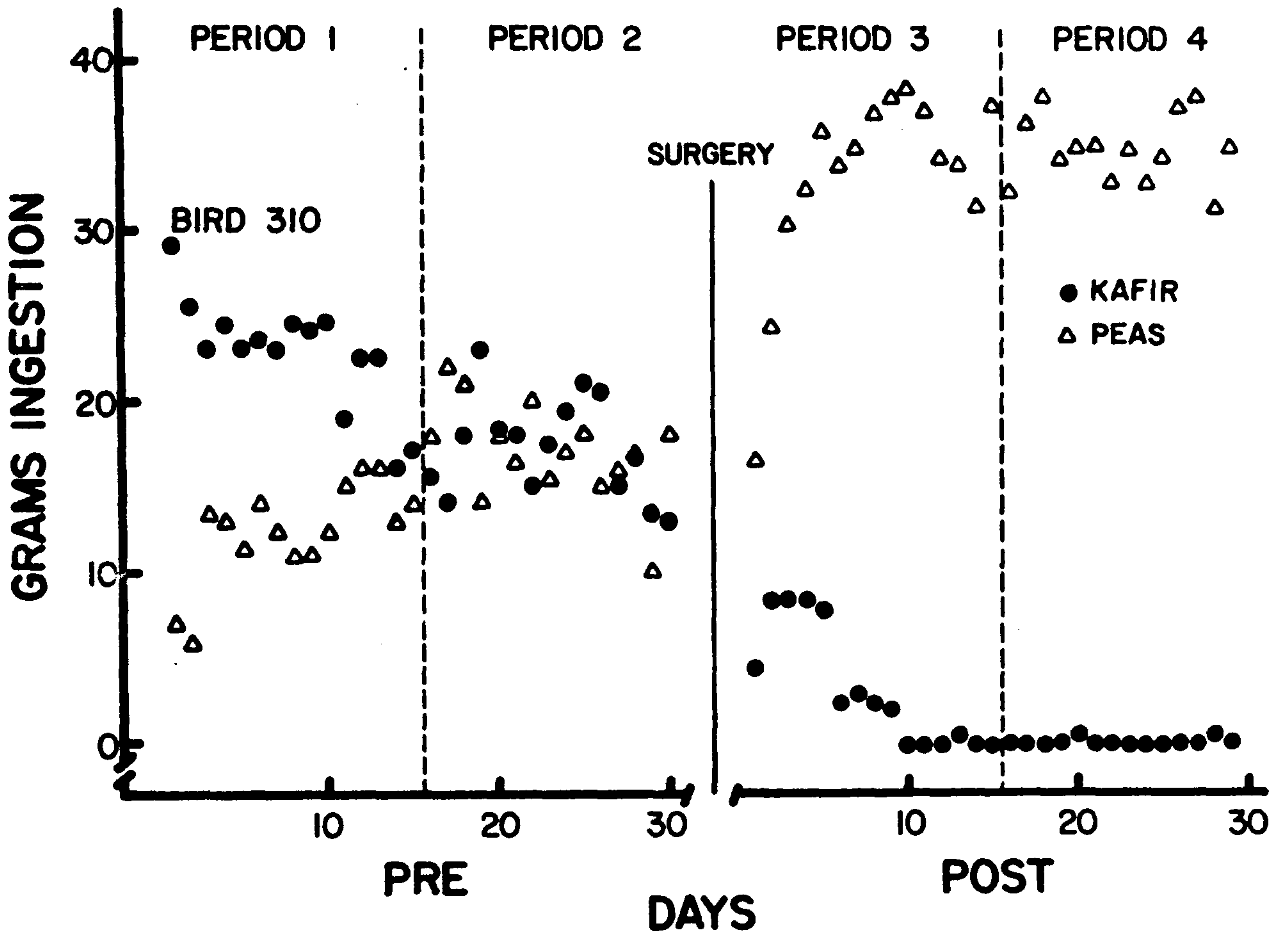


FIG. 9. Seed ingestion(g) by bird 310 pre- and postoperatively. Kafir and peas were offered *ad libitum*. Periods 1, 2, and 3 were 15 days each. Period 4 was 14 days. This bird sustained a one-branch trigeminal lesion.

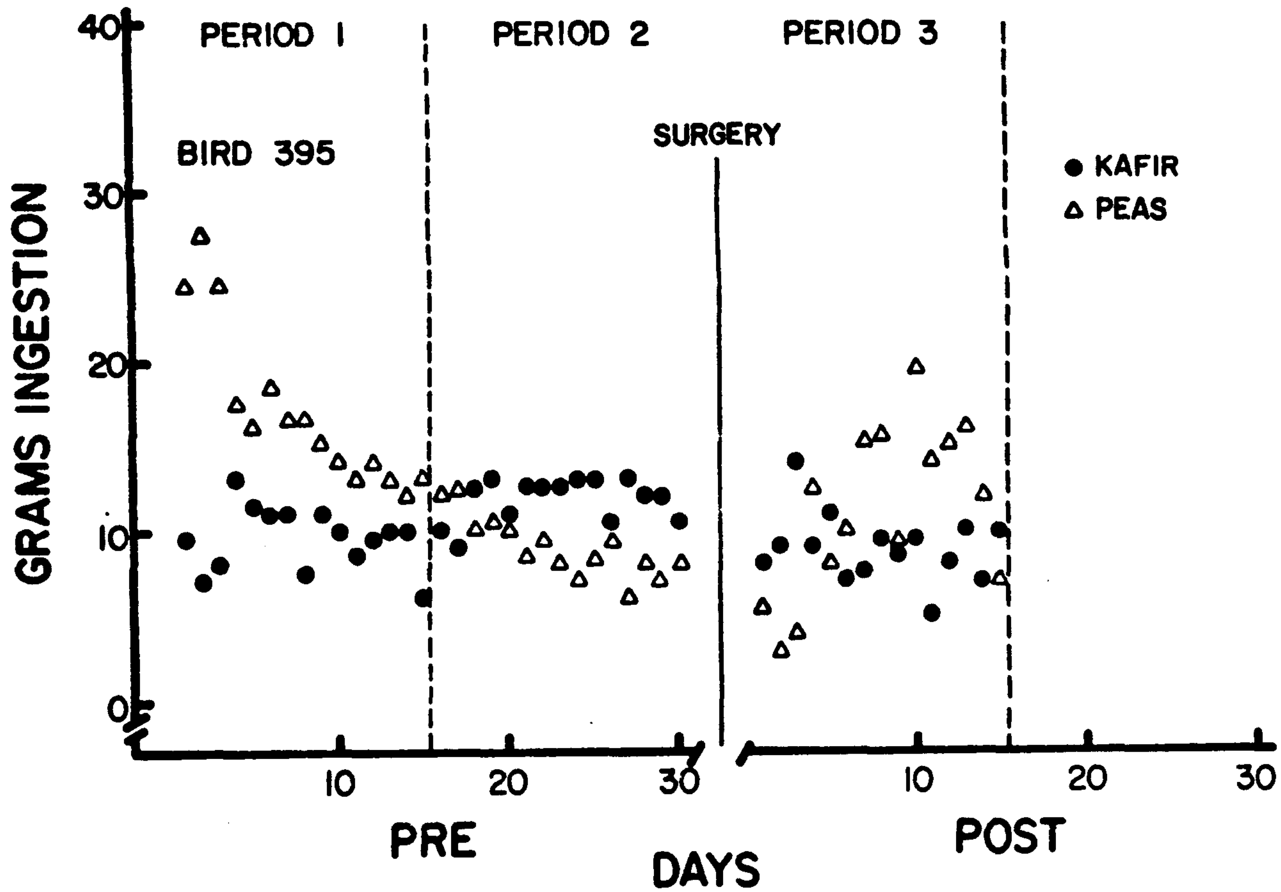


FIG. 10. Seed ingestion(g) by bird 395 pre- and postoperatively. Kafir and peas were offered ad libitum during (only) 3 consecutive 15-day periods. This bird sustained a two-branch trigeminal lesion.

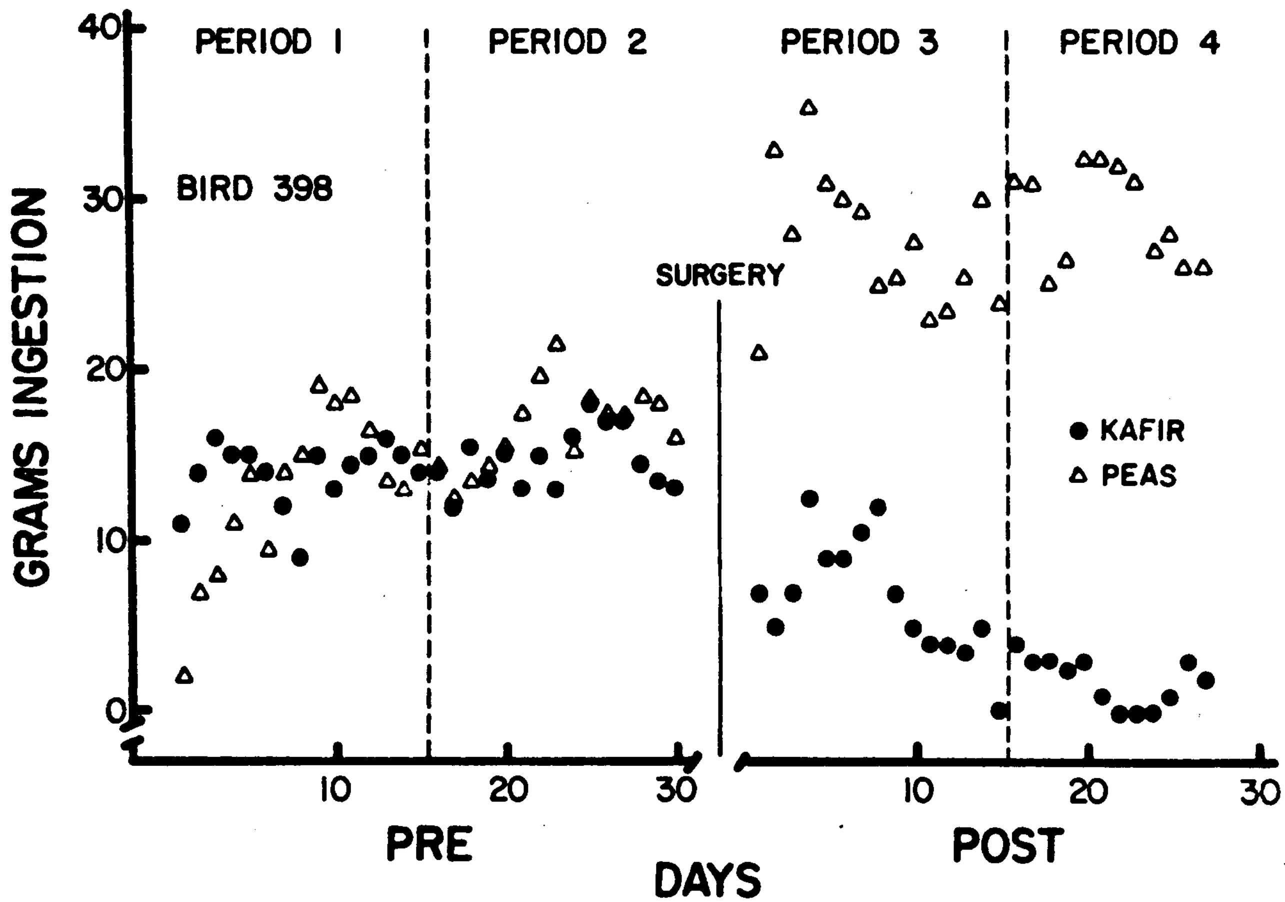


FIG. 11. Seed ingestion(g) by bird 398 pre- and postoperatively. Kafir and peas were offered ad libitum. Periods 1, 2, and 3 were 15 days each. Period 4 was 12 days. This bird sustained a one-branch trigeminal lesion.

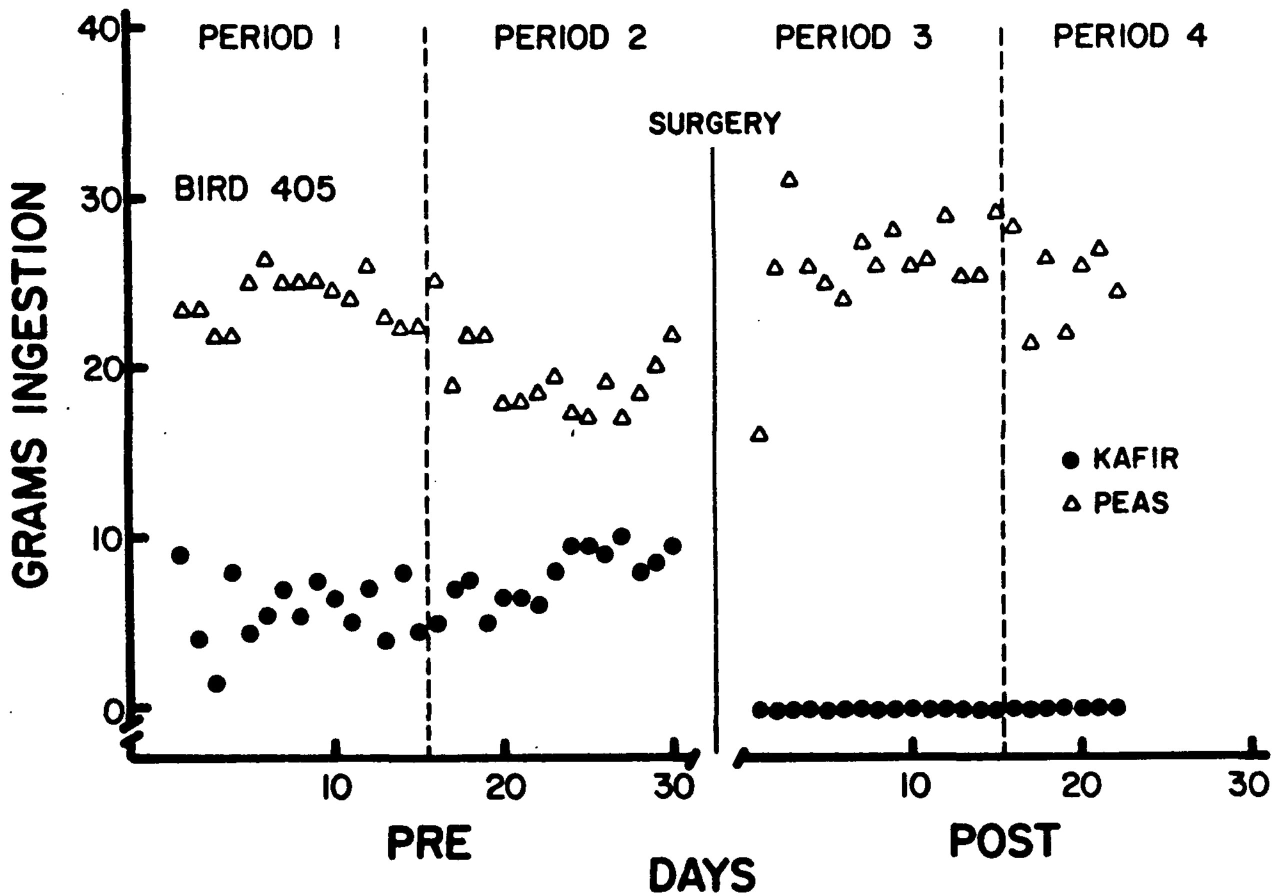


FIG. 12. Seed ingestion(g) by bird 405 pre- and postoperatively. Kafir and peas were offered ad libitum. Periods 1, 2, and 3 were 15 days each. Period 4 was 7 days. This bird sustained a two-branch trigeminal lesion.

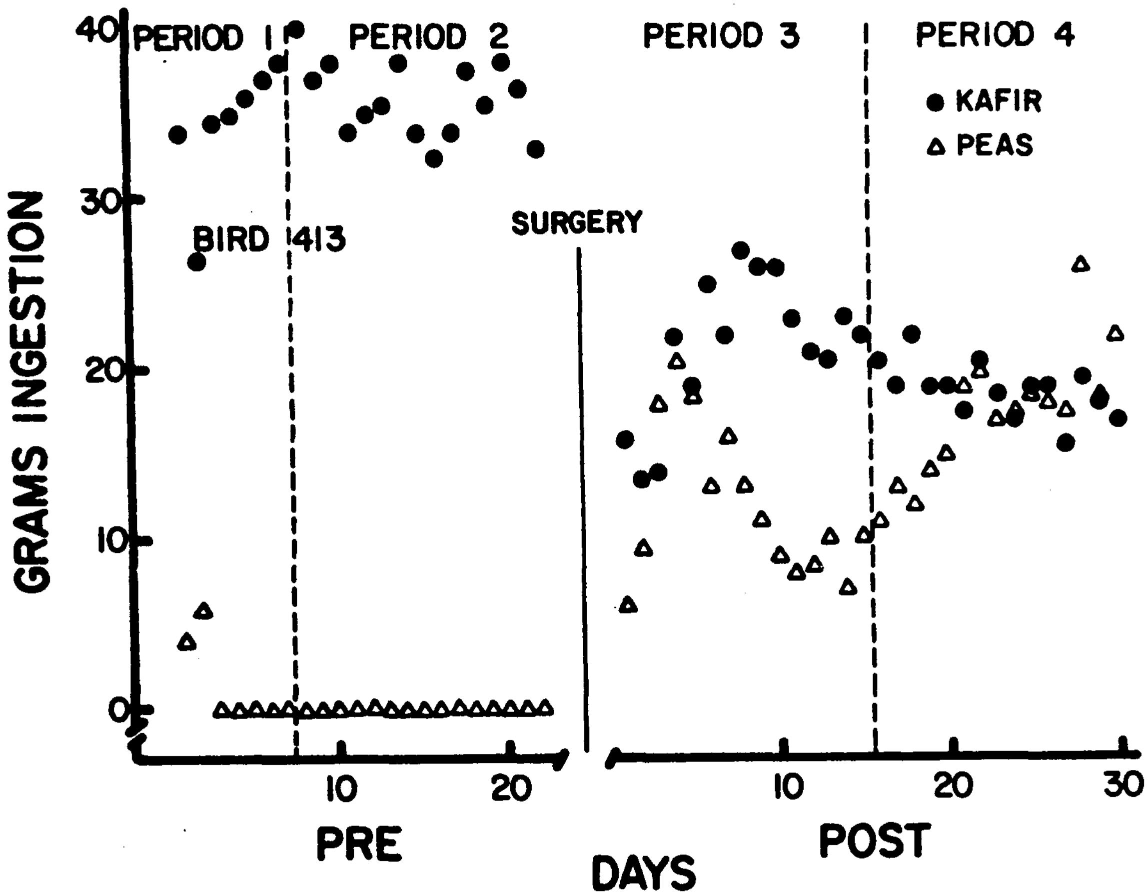


FIG. 13. Seed ingestion(g) by bird 413 pre- and postoperatively. Kafir and peas were offered ad libitum. Period 1 was 8 days. Periods 2, 3, and 4 were 15 days each. This bird sustained a one-branch trigeminal lesion.

24 and 25) showed there was no relationship between the kinds of seeds offered or eaten and the changes in total intake seen in the preoperative period. Birds 392, 393, 395, 400 and 507 ingested less food in period 2 than in period 1 while birds 377, 398 and 399 ingested significantly more food in the second period. All other birds ingested similar amounts of food in periods 1 and 2.

Birds 392, 507, and 526 ingested less food in period 3 than in period 2 and birds 392, 393 and 394 ingested less food in period 4 than in period 3. All other birds ingested similar amounts of food in periods 2, 3, and 4. These data for total food intake in periods 3 and 4 and data presented above on the recovery of body weight (see Table 2) confirm that (with the exception of bird 377) all birds subjected to the surgical procedures for two-branch trigeminal deafferentation were hypophagic in periods 3 and 4: they did not show significant compensatory increases in food intake even though they remained below their mean *ad libitum* body weight for period 2.

Effects of Deafferentation on Water Intake

The data and results of statistical analyses for water intake (Tables Z-BB) show that water intake varied considerably and that there was no clear relationship between changes in water intake and the kinds of seeds eaten or the extent of deafferentation.

Effects of Deafferentation on Body Weight

Most birds (1) decreased their weight, or showed no changes in body weight before surgery, (2) lost weight in period 3 and remained at this lower level of body weight, or regained some, but not all, of the previously lost body weight in the fourth period (see Tables S-U).

All birds except 310, 395 and 392 increased their body weight or showed no changes in body weight in period 2 re period 1.

After surgery all birds (except 310, 377, 398 and 399) had a significantly lower mean weight in period 3 than in period 2. Four of the animals which lost body weight after surgery (306, 392, 400, and 405) did not regain their weight in the fourth period and thus had a significantly decreased weight in both periods 3 and 4. The other birds which lost weight in period 3 gained weight in period 4 so that their mean body weight in the fourth period exceeded that of period 3. Only bird 413 gained a sufficient amount of weight in the fourth period to reach the period 2 weight: birds 306, 341, 392, 393, 400 and 405 failed to reach their period 2 body weight within the period of time in which data was collected.

Discussion

The pigeons subjected to the surgical procedures for bilateral section of the ophthalmic and mandibular trigeminal branches showed periods of aphagia and hypophagia characteristic of the trigeminal syndrome. Most of these birds also showed changes in the ingestion of seeds which appeared to be directly related to seed size regardless of the extent of the lesion sustained (i.e., one- or two-branch) or the number or kinds of seeds presented. Kafir, the smallest seed, was ingested in decreased amounts while larger seeds were ingested in increased amounts postoperatively.

The changes in seed ingestion observed after deafferentation are probably not related to the loss of body weight the birds sustained during the aphagic period following surgery. The results presented in III D above suggest that deprivation leads to an increase in kafir intake and no absolute change but a relative decrease in peas intake. The deafferented birds generally showed both an absolute and a relative increase in peas intake: peas intake increased while total intake did not change. The changes observed also cannot be explained as a postsurgical "finickiness" which leads to a greater intake of highly palatable foods and/or a decreased intake of less "palatable" foods comparable to that seen in the rat after lesions of the lateral or ventromedial hypothalamus. There is no evidence which suggests kafir is less "palatable" or that peas are more "palatable" than the other seeds offered. In fact, the lack of peas intake in the presurgical period by birds 394 and 413 could suggest that this food was aversive to these birds (cf. Rozin & Kalat, 1971).

The changes in seed ingestion seen after one-branch and two-branch deafferentation are, perhaps, best understood in light of data from previous studies indicating that the trigeminally deafferented pigeon is less efficient when eating small grains (i.e., milo). Inspection of the curves for the deafferented birds fed kafir, a seed which is the same size as milo, and peas, shows the kafir intake of two birds (310, 398) declined over a period of several days, while peas intake increased almost immediately after surgery (see Figures 9 and 11). These curves for kafir intake may reflect a difficulty in obtaining kafir and subsequently, an extinction of consummatory responses directed toward kafir. This suggestion is further supported by the curves for bird 413 (Figure 13). A presumed decreased number of successful consummatory responses directed toward kafir could result in the extinction of these responses, while a relatively larger number of successful responses directed toward peas could increase the number of responses so directed. The preoperative levels of ingestion complicate, but do not contradict, this interpretation. That is, the relative efficacy of consummatory responses can not fully account for the relative ingestion of different seeds because birds continue to ingest small seeds after deafferentation, even though the immediate postsurgical ingestion of several subjects (see Group KP) would suggest that peas are more readily consumed. On the other hand, there may be no changes in the relative postsurgical seed ingestion when the presurgical ingestion happens to be directly related to seed size (e.g., corn and vetch; bird 393, Figure 5). In cases where the seeds eaten are of a more similar size than kafir and peas (e.g., hemp and vetch, bird 400; see Table 1) trigeminal damage may lead to more nearly equal ingestion. Thus, the intake of seeds after trigeminal damage may generally be proportionate with the size of the seeds eaten with large seeds being eaten in greater amounts than small seeds.

Relationships Between General Responsiveness and the Efficiency of Seed Ingestion

The two-branch lesions in the present study and in previous studies led to a postsurgical hypophagia manifested as a failure to eat sufficient amounts of food to compensate for lost body weight. In previous studies small grains, "Columbia Special" seed mixture or milo, were offered *ad libitum*. Thus, the decreased efficiency of feeding on small grains may have led to the maintenance of a lower body weight. In the present experiment two-branch birds were offered both small seeds and large seeds (e.g., peas), which weighed an average of .5 grams. Judging by the postsurgical responses, these peas were obtainable and would seem to have allowed a very rapid recovery of body weight (cf. bird 508, Section III D). As the two-branch deafferented birds did not eat sufficient peas to regain their body weight, it would appear that the hypophagia observed cannot be completely explained by a decreased efficiency of feeding. Experiments in which the size and caloric content of foods are manipulated independently would elucidate the relationships between efficiency and responsiveness to food.

IV B

Effects of Nucleus Basalis Lesions on the Differential Ingestion of Seeds

As nucleus basalis (NB), the major telencephalic nucleus of the trigeminal "feeding system," is an indirect recipient of afferent fibers from the trigeminal sensory branches, NB lesions may also alter the differential ingestion of seeds (See Sections III and IV A).

Methods and Procedures

Subjects

The subjects were seven experimentally naive adult male and female White Carneaux pigeons adjusted to the laboratory and maintained on a regimen described above in General Methods and Procedures.

Feeding Procedures

The seven birds were offered hemp, kafir, and peas *ad libitum* for 30-35 days before and after electrolytic lesions were placed as described below. The seeds were presented and all measures were taken in the usual manner.

Surgical Procedures

One or two birds were lesioned on each of several days during a two week period. Each bird was deprived of food from 4:30 p.m. the day before surgery until immediately after the surgery, which was conducted before 4:30 p.m. the following day.

Each bird was anesthetized with Equithesin (2.0 ml/kg), the feathers were cut from the top of its head, and it was positioned in a Kopf stereotaxic device. A midline incision was made and the scalp was drawn laterally exposing the skull surface. A small hole was drilled through the skull on each side of the midline suture at appropriate coordinates and the dura was punctured. Anodal electrolytic lesions were made with a DC lesion maker and 00 insect pins coated to within 0.5 mm of the tip with Insulex at the coordinates shown in Table 28. Then the holes in the skull were covered with gelfoam, the incision was closed with surgical wound clips, and the subject was returned to its cage where food and water were available *ad libitum*.

Histology and Ratings of Damage to Nucleus Basalis

Approximately 30 days after surgery the birds were anesthetized and perfused intracardially with physiological saline and 10 per cent formalin in saline. The brains were blocked in the sterotaxic plane, removed from the skull, and embedded in celloidin. Alternate serial sections cut at 30 U were mounted and stained for cells

Table 28

Coordinates, Amperage and Duration of Intended Lesions

Bird Numbers	Lesion	AP	ML	DV	Seconds	Milliamps
9	NB	12.0	4.5	7.0	60	2
		12.5	3.0	6.5	60	2
		12.5	4.0	7.0	60	2
316	NB	12.0	4.5	7.0	60	2
		12.5	3.0	6.5	60	2
		12.5	4.0	7.0	60	2
329	NB	12.0	4.5	7.0	60	2
		12.5	3.0	6.5	60	2
335	HvDv	12.0	4.0	11.0	30	2
370	LPO	11.5	2.0	7.0	30	2
376	NB	12.0	4.5	7.0	60	2
		12.5	3.0	6.5	60	2
		12.5	4.0	7.0	60	2
382	NB	12.0	4.5	7.0	60	1
		12.5	3.0	6.5	60	1
		12.5	4.0	7.0	60	1

Note. NB=nucleus basalis, HvDv=hyperstriatum ventrale dorsoventrale, LPO= lobus parolfactorius. Figures below AP, ML and DV indicate the distance (mm) of the intended lesion from the Antero-posterior, medio-lateral, and dorso-ventral planes according to the atlas of Karten & Hodos (1967).

and fibers by the Kluver-Barrerra Method. Professor H.P. Zeigler rated the NB damage of each subject on a scale of 1 to 3 by visual inspection without knowledge of the behavioral results (Zeigler, 1974a). The extent of the damage to structures surrounding NB and to areas of the hyperstriatum ventrale ventroventrale (HVvv) and lobus parolfactorius (LPO) (Karten and Hodos, 1967) was also determined for all subjects.

Data Analyses

The pre- and postoperative data for subjects sustaining electrolytic lesions of NB were analyzed in the same manner as the data for deafferented subjects presented above (Section IV A). Statistical analyses were computed on all measures taken in the first and second 15 preoperative days (period 1 and period 2, respectively) and these data were then compared with those of the first and second 15 postoperative days, period 3 and period 4. (The data for birds 329 and 370, were analyzed similarly even though there were only 28, and 29 days of postoperative data, respectively.)

Results

Extent of Damage to Nucleus Basalis (NB)

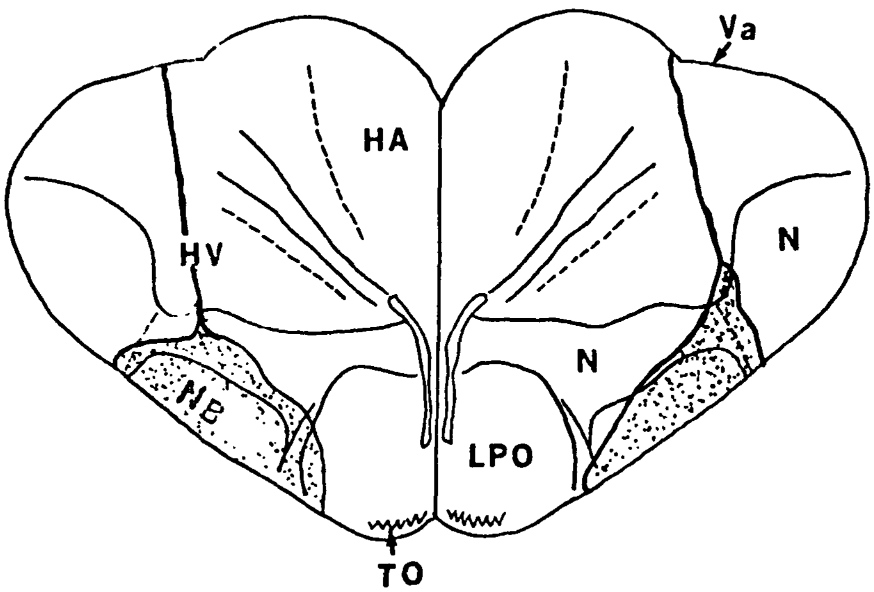
Table 29 shows the ratings assigned to the NB lesions and Figures 14 through 20 show coronal reconstructions of the maximum extent of damage to NB, HVvv, and LPO. The NB lesions were of small to moderate size, and, excluding birds 9 and 329, bilateral. While the ratings suggest there was little damage to NB, the damage must be viewed in perspective with the large size of NB, which extends approximately 2 mm in the antero-posterior plane. Because of its large size it is seldom totally destroyed, and when damage is nearly total, infarctions interfere with the histological analysis (Zeigler & Karten, 1973a). Birds 316, 376, and 382 (Figures 14-16) sustained small to moderate, bilateral damage to NB, extending from approximately A 13.25 - 13.0 to A 10.75 - 10.50. There was additional damage to the fronto-archistriate tract (FA), neostriatum (N) and paleostriatum augmentatum (PA) of bird 382; to the ectostriatum (E), FA, hyperstriatum ventrale dorsoventrale (HvDv), HVvv, LPO, and PA of bird 376, and to E, hyperstriatum dorsale (HD), hyperstriatum intercalatus superior (His), HvDv, HVvv, and N of bird 316. Birds 9 and 329 (Figures 17 and 18) sustained only or primarily unilateral NB damage. Since successive electrode placements were made with great care this unexpected unilateral damage suggests inadequate grounding and/or malfunctioning of the lesion maker. Bird 329 sustained moderate NB damage in the right hemisphere at approximately A 12.5 - A 10.75; additional damage to HVvv, lamina hyperstriatica

Table 29

Ratings Assigned to the Damage of Nucleus Basalis

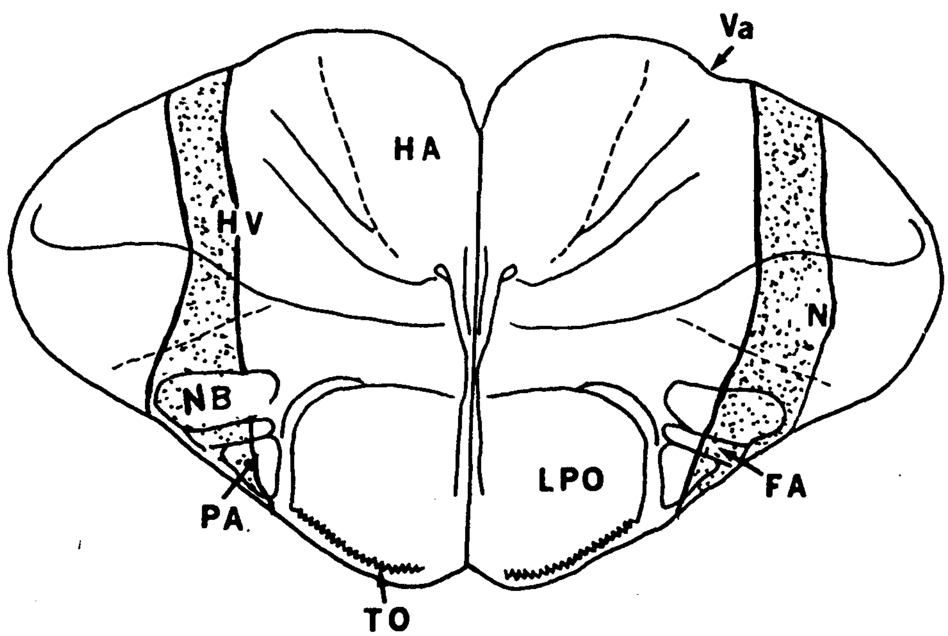
Bird Numbers	Left Hemisphere	Right Hemisphere
316	2	2
376	2-3	1
382	1	1-2
329	0-1	2
9	0	1
335	0	0
370	0	0

Note. 0 indicates no damage, 1=small, 2=moderate, 3=complete.



A 12.50 Bird 316

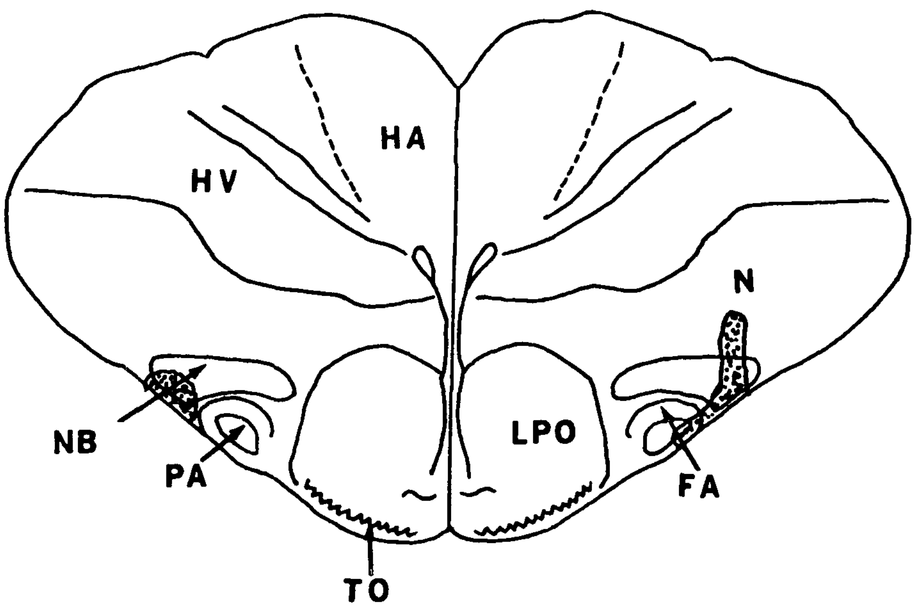
Fig. 14. Schematic representation (after Karten & Hodos, 1967) of the maximum extent of damage (stippled area) to nucleus basalis (NB) of bird 316. The figure at the left is the antero-posterior coordinate. The rating assigned to NB damage was: left hemisphere, 2; right hemisphere, 2 (see text). This subject sustained moderate bilateral damage to NB and to areas His, HvDv, and N (see List of Abbreviations in the Appendix).



A 11.75 Bird 376

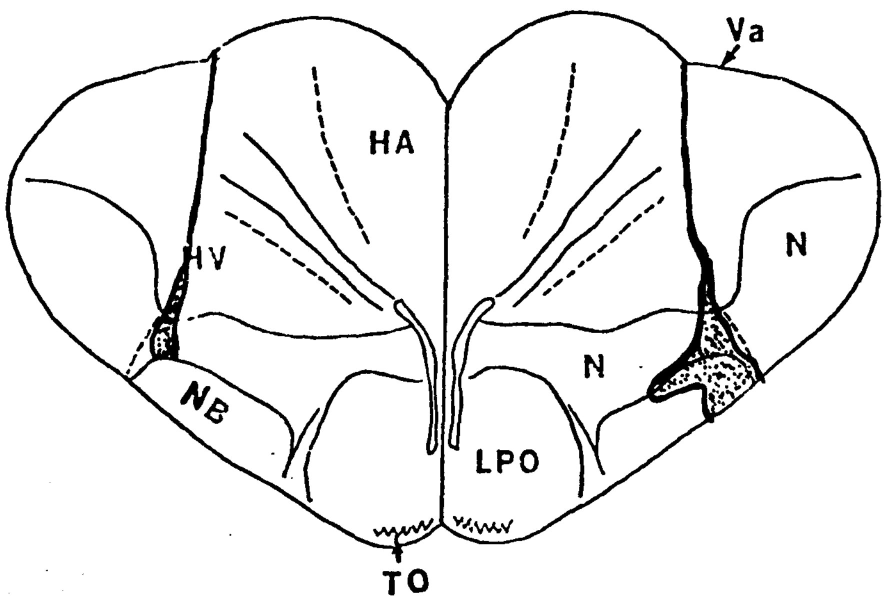
Fig. 15. Schematic representation (after Karten & Hodos, 1967) of the maximum extent of damage (stippled area) to nucleus basalis (NB) of bird 376. The figure at the left is the antero-posterior coordinate. The rating assigned to the NB damage was: left hemisphere, 2-3; right hemisphere, 1 (see text). This subject sustained moderate to total NB damage in the left hemisphere, a small amount of NB damage in the right hemisphere, and additional damage to E, FA, HvDv, HVvv, LPO, and PA (see List of Abbreviations in the Appendix).

15 9



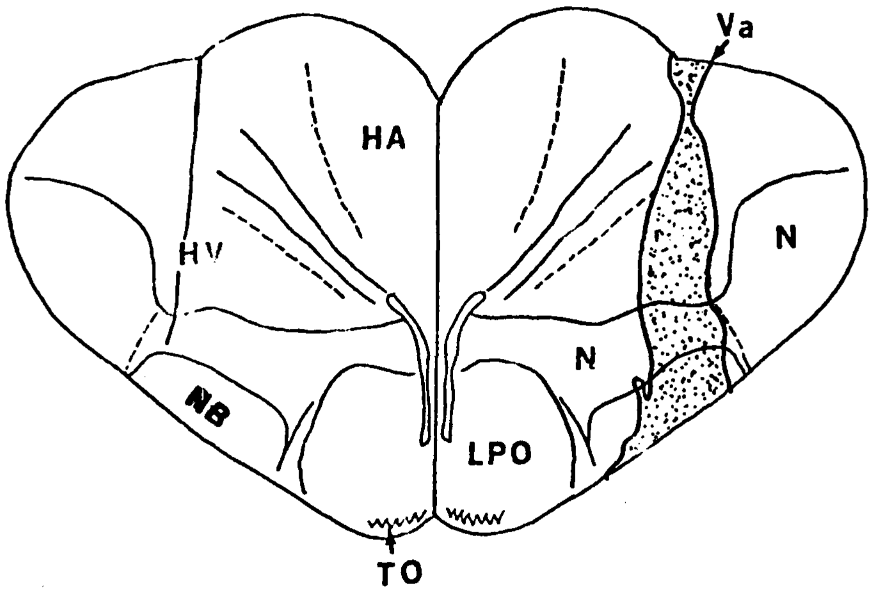
A 12.00 Bird 382

Fig. 16. Schematic representation (after Karten & Hodos, 1967) of the maximum extent of damage (stippled area) to nucleus basalis (NB) of bird 382. The figure at the left is the antero-posterior coordinate. The rating assigned to NB damage was: left hemisphere, 1; right hemisphere, 1-2 (see text). This subject sustained small to moderate bilateral NB damage and damage to FA, N, and PA (see List of Abbreviations in the Appendix).



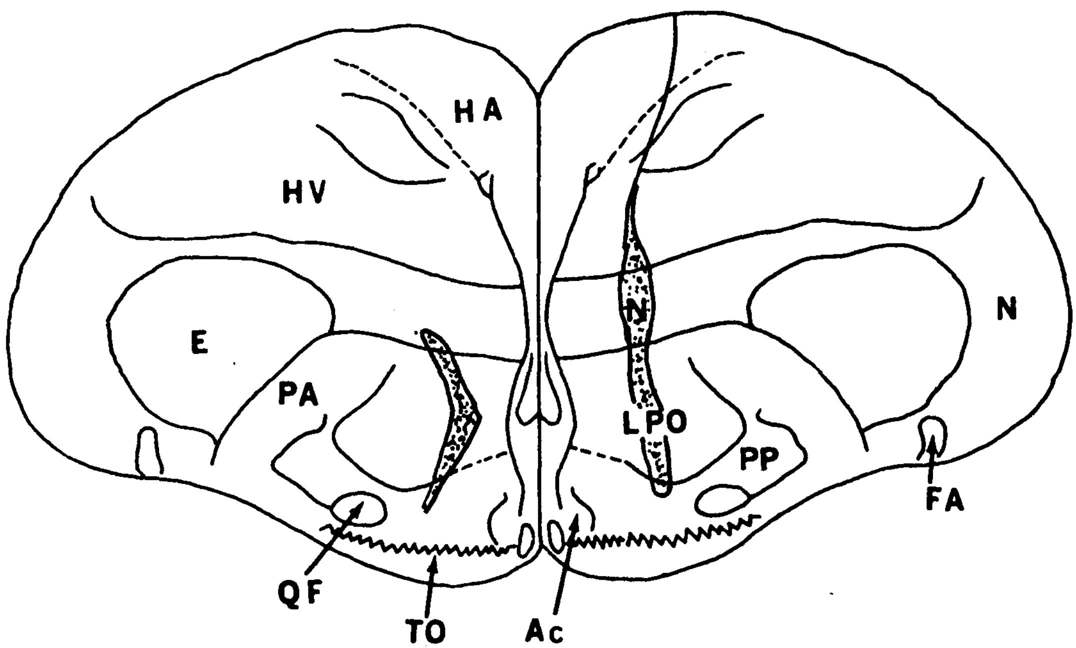
A 12.50 Bird 9

Fig. 17. Schematic representation (after Karten & Hodos, 1967) of the maximum extent of damage (stippled area) to nucleus basalis (NB) of bird 9. The figure at the left is the antero-posterior coordinate. The rating assigned to NB damage was: left hemisphere, 0; right hemisphere, 1 (see text). This subject sustained a small unilateral NB lesion, and additional damage to areas of HVvv, HV, LH, N, FA, and PA in the right hemisphere (see List of Abbreviations in the Appendix).



A 12.50 Bird 329

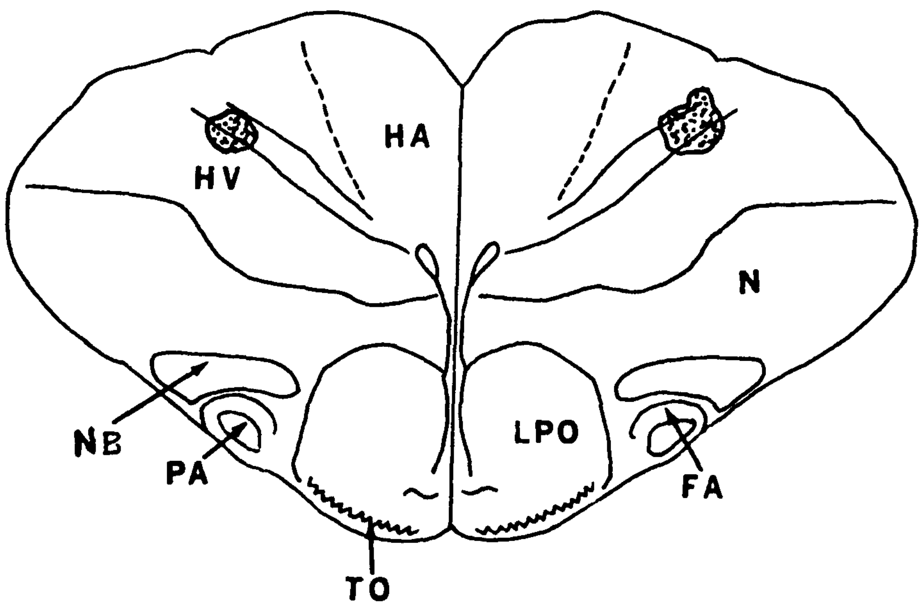
Fig. 18. Schematic representation (after Karten & Hodos, 1967) of the maximum extent of damage (stippled area) to nucleus basalis (NB) of bird 329. The figure at the left is the antero-posterior coordinate. The rating assigned to NB damage was: left hemisphere, 0-1; right hemisphere, 2 (see text). This subject sustained little or no damage to the left hemisphere, moderate to total damage of the right hemisphere, and additional damage to areas of HVvv, LH, and N (see List of Abbreviations in the Appendix).



A 11.00 Bird 370

Fig. 19. Schematic representation (after Karten & Hodos, 1967) of the maximum extent of damage (stippled area) to lobus parolfactorius (LPO) of bird 370. The figure at the left is the antero-posterior coordinate. The rating assigned to NB damage was: left hemisphere, 0; right hemisphere, 0 (see text). This subject sustained moderately large LPO lesions and damage to MD and N but no NB damage (see List of Abbreviations in the Appendix).

163



A 12.00 Bird 335

Fig. 20. Schematic representation (after Karten & Hodos, 1967), of the maximum extent of damage (stippled area) to the hyperstriatal areas of bird 335. The figure at the left is the antero-posterior coordinate. The rating assigned to NB damage was: left hemisphere, 0; right hemisphere, 0 (see text). This subject sustained bilateral damage to His, HV, and HvDv, and no NB damage (see List of Abbreviations in the Appendix).

(LH) and N; and very minor NB damage in the left hemisphere. The NB lesion of bird 9 was in the right hemisphere extending approximately from A 13.5 to A 0.25. Additional damage was seen in the areas of FA, hyperstriatum ventrale (HV), HVvv, LH, N and PA. The trace of an electrode track directed toward NB was seen in the left hemisphere at approximately A 12.75.

The control lesions successfully damaged structures adjacent (bird 370, Figure 19) or dorsal (bird 335, Figure 20) to NB while leaving NB intact (Table 29). The lesions of bird 370 were moderately large and placed well into LPO, medial to the quinto-frontal tract (QFT), and lateral to the ventricles. They extended from approximately A 11.25 to A 10.25 and damaged areas of medullaris dorsalis (MD), and N, but not NB. Bird 335 sustained very small bilateral lesions in the general areas of His, HV and HvDv, dorsal to NB.

Recovery of Food Intake and Body Weight

Previous research has shown that birds sustaining moderate to total bilateral NB lesions (i.e., ratings of 2 to 3 in both hemispheres) are generally aphagic for several days after surgery and do not regain their pre-operative *ad libitum* body weight for several weeks (Zeigler & Karten, 1974a). Table 30 shows that only bird 316, which sustained the largest bilateral lesions, was aphagic, but all animals remained below their period

Table 30

Effects of Nucleus Basalis Lesions on Food Intake, Body Weight Loss, and Body Weight Recovery

Bird Numbers	Rating Assigned to NB Damage		Days of Aphagia	Number of Days Below 50% of Mean Period 2 Food Intake	Number of Postsurgical Days Below Period 2 BW[a]
	LH	RH			
316	2	2	2	5	33*
376	2-3	1	0	2	33*
382	1	1-2	0	1	32*
329	0-1	2	0	1	28
9	0	1	0	0	32*
335	0	0	0	1	33*
370	0	0	0	1	16

Note. LH=left hemisphere, RH=right hemisphere, O=no damage, 1=small, 2=moderate, and 3=complete damage. Subjects 335 and 370 were control animals which sustained damage to areas medial or dorsal to nucleus basalis (NB). Asterisks indicate the last day data were collected.

[a] BW = Body Weight.

2 mean *ad libitum* weight during periods 3 and/or 4. Bird 370, which had damge to LPO, and no visible damage to NB, recovered its body weight in 16 days. As animals which sustain damage to QFT, the primary NB afferent, are aphagic and require several weeks to recover their preoperative body weight (Zeigler & Karten, 1974a), as are birds with large NB lesions, it is clear that neither QFT nor NB was damaged. Birds sustaining primarily unilateral NB damage remained below their period 2 *ad libitum* body weight about the same number of days as birds which sustained bilateral NB damage. Birds 335 and 376, which sustained bilateral damage, did not recover their *ad libitum* body weight during the observation period. However, this criterion is not useful for these subjects because they lost weight prior to surgery.

Analyses of the data for total food intake (presented in detail below) showed that all subjects with bilateral NB lesions failed to increase their food intake to compensate for their lost body weight.

Effects of Nucleus Basalis Lesions on Seed Ingestion

Changes in the Kinds of Seeds Eaten. All subjects, except bird 376, which sustained moderate bilateral damage to NB, ate the same kinds of seeds in all 4 periods (Table 31). The postoperative changes in the seed ingestion of bird 376 are presented in detail with those of other subjects below.

Table 31

Kinds of Seeds Eaten in 15 Day Periods Before and After Nucleus Basalis (NB) Lesions

Bird Numbers	Rating Assigned to NB Damage LH	RH	PRE Period 1	Period 2	POST Period 3	Period 4
316	2	2	HK	HK	HK	HK
376	2-3	1	KP	KP	HKP	KP
382	1	1-2	HK	HK	HK	HK
329	0-1	2	HK	HK	HK	HK
9	0	1	HK	HK	HK	HK
335	0	0	HK	HK	HK	HK
370	0	0	KP	KP	KP	KP

Note. LH = left hemisphere, RH = right hemisphere, 0 indicates no damage, 1 = small, 2 = moderate, and 3 = complete damage. Subjects 335 and 370 were control animals which sustained damage to areas medial or dorsal to nucleus basalis (NB). Hemp (H), Kafir (K) and Peas (P) were offered *ad libitum* during periods 1, 2, 3 and 4.

<u>Changes in the Differential Ingestion of Seeds</u>. Tables 32 and 33 show the medians and ranges for the pre- and postoperative ingestion of each seed and Table 34 summarizes the results of statistical analyses of the seed ingestion data (Table 35). Collectively, these indicate that six birds had changes in the differential ingestion of seeds which were due to postoperative changes in kafir and/or hemp intake. The nature of the post-surgical changes in the intake of these seeds is not readily seen in the data presented for periods. Therefore, daily data are provided and described for each subject below. It will be seen that all birds which sustained bilateral NB damage significantly decreased kafir intake and/or increased hemp intake during period 3. Some birds recovered their preoperative levels of hemp and kafir intake after only a few days while other birds, which sustained larger lesions did not resume their preoperative intake. Birds which sustained damage to LPO and HVvv and no NB damage showed transient departures from the preoperative levels of hemp and kafir intake (bird 335) or showed changes in seed ingestion unlike the changes seen for the birds with NB damage (bird 370).

<u>Postoperative Decreases in Kafir Intake</u>. Bird 316 (Figure 21) ate equal amounts of hemp and kafir in periods 1 and 2. After sustaining moderate, bilateral

Table 32

Medians and Ranges for the *Ad libitum* Ingestion(g) of Hemp(H), Kafir(K) and Peas(P) During 15 Day Periods Before Nucleus Basalis Lesions

Bird Numbers	Rating Assigned to NB Damage: LH	RH	Seed[a]	Period 1 Median	Period 1 Range	Period 2 Median	Period 2 Range
316	2	2	H	16.3	13.0-22.0	15.8	10.0-27.0
			K	14.0	3.0-19.0	14.7	6.0-18.5
			Total	30.0	19.0-37.0	30.0	16.0-42.0
376[a]	2-3	1	H	-	-	-	-
			K	22.6	19.0-27.5	24.4	11.0-29.0
			P	7.0	4.0-13.0	5.7	2.5-11.0
			Total	30.0	26.0-35.0	30.3	26.0-36.0
382	1	1-2	H	9.8	5.0-14.5	9.6	4.0-19.0
			K	14.8	9.0-17.5	16.0	10.0-23.0
			Total	24.6	18.0-28.5	24.3	19.0-42.0
329	0-1	2	H	8.7	4.0-15.0	10.8	7.0-18.0
			K	25.5	19.0-32.0	23.3	14.0-32.0
			Total	25.3	27.0-38.0	36.0	25.0-50.0
9	0	1	H	10.1	8.0-15.0	9.8	6.0-15.0
			K	16.3	9.0-20.5	15.6	11.5-19.0
			Total	27.0	23.5-30.5	25.8	19.5-30.0
335	0	0	H	13.0	10.0-18.0	13.7	7.0-20.0
			K	10.4	5.0-17.0	13.7	7.0-19.0
			Total	24.0	17.0-30.0	26.0	21.0-34.0
370	0	0	K	9.5	5.5-12.0	9.8	6.0-21.0
			P	23.0	19.0-28.0	20.4	13.0-29.0
			Total	32.8	27.5-38.0	33.8	24.0-41.0

Table 32 (continued)

Note. LH = left hemisphere, RH = right hemisphere, 0 indicates no damage, 1 = small 2 = moderate, and 3 = complete damage. Subjects 335 and 370 were control animals which sustained damage to areas medial or dorsal to nucleus basalis (NB).

[a] Bird 376 ate hemp in period 3 but not in periods 1 and 2.

Table 33

Medians and Ranges for the *Ad libitum* Ingestion(g) of Hemp(H), Kafir(K) and Peas(P) During 15 Day Periods After Nucleus Basalis Lesions

Bird Numbers	Rating Assigned to NB Damage: LH	Rating Assigned to NB Damage: RH	Seed[a]	Period 3: Median	Period 3: Range	Period 4: Median	Period 4: Range
316	2	2	H	18.5	9.0-28.0	23.3	12.0-29.5
			K	6.8	0.0-14.0	5.0	0.5-11.5
			Total	21.8	16.5-34.5	27.3	17.0-33.0
376[a]	2-3	1	H	3.0	0.0-23.0	-	-
			K	13.0	0.0-25.0	16.0	8.5-24.0
			P	10.0	0.0-22.0	12.3	8.0-26.0
			Total	26.0	17.0-39.5	31.5	26.5-37.0
382	1	1-2	H	14.7	8.0-20.0	10.8	5.5-16.0
			K	10.4	4.0-18.5	12.3	6.0-16.5
			Total	25.7	16.0-30.5	22.3	17.5-29.0
329	0-1	2	H	11.3	2.0-23.0	11.5	8.0-20.0
			K	18.0	13.0-28.0	26.0	19.0-30.5
			Total	29.0	19.0-42.0	37.5	30.5-44.5
9	0	1	H	13.0	9.0-17.5	8.5	3.0-17.0
			K	13.0	1.0-18.0	13.1	8.0-20.0
			Total	25.8	18.0-33.0	25.0	16.5-27.5
335	0	0	H	16.7	0.5-26.0	10.2	5.0-17.0
			K	8.8	2.5-15.0	8.3	4.0-14.0
			Total	24.0	14.0-30.0	19.3	12.0-28.0
370	0	0	K	18.8	11.0-32.0	7.3	3.0-19.0
			P	15.3	0.0-24.5	22.8	6.0-29.0
			Total	34.1	16.5-43.0	31.0	25.0-33.0

Table 33 (continued)

Note. LH = left hemisphere, RH = right hemisphere, 0 indicates no damage, 1 = small 2 = moderate, and 3 = complete damage. Subjects 335 and 370 were control animals which sustained damage to areas medial or dorsal to nucleus basalis (NB).

[a] Bird 376 ate hemp in period 3 but not in period 4.

Table 34

Differential Ingestion of Hemp(H), Kafir(K) and Peas(P) in 15 Day Periods Before and After Nucleus Basalis Lesions

Bird Numbers	Rating Assigned to NB Damage LH	RH	PRE Period 1	Period 2	POST Period 3	Period 4
316	2	2	H=K	H=K	H>K	H>K
376	2-3	1	K>P	K>P	H=K=P	K=P
382	1	1-2	K>H	K>H	H=K	H=K
329	0-1	2	K>H	K>H	K>H	K>H
9	0	1	K>H	K>H	H=K	K>H
335	0	0	H>K	H=K	H>K	H=K
370	0	0	P>K	P>K	K>P	P>K

Note. LH = left hemisphere, RH = right hemisphere, 0 indicates no damage, 1 = small, 2 = moderate, and 3 = complete damage. Subjects 335 and 370 were control animals which sustained damage to areas medial or dorsal to nucleus basalis (NB). Relationships shown are the results of Friedman and/or Wilcoxon tests. Equal signs indicate $p > .05$.

Table 35

Mann-Whitney U Tests on Seed Ingestion in 15 Day Periods Before and After Nucleus Basalis Lesions

Bird Numbers	Rating Assigned to NB Damage		Seed[a]	Direction of Differences					
	LH	RH		1vs.2	2vs.3	3vs.4	1vs.4	2vs.4	1vs.3
316	2	2	H	-	-	-	-	-	-
			K	1=2	2>3***	3=4	1>4***	2>4***	1>3**
			Total	1=2	2>3**	3=4	1>4*	2>4***	1>3*
376	2-3	1	H	1=2	2<3**	3>4*	1=4	2=4	1<3*
			K	1<2*	2>3***	3<4*	1>4***	2>4***	1>3***
			P	-	-	3=4	1<4***	2<4***	-
			Total	-	-	-	-	-	-
382	1	1-2	H	1=2	2<3***	3>4**	1=4	2=4	1<3***
			K	1=2	2>3**	3=4	1>4*	2>4***	1>3*
			Total	-	-	-	1=4	-	-
329	0-1	2	H	-	-	-	1<4**	-	-
			K	1=2	2>3*	3<4**	1=4	2=4	1>3**
			Total	1=2	2>3*	3<4**	1<4**	2=4	1=3
9	0	1	H	1=2	2<3*	3>4**	1>4*	2=4	1<3*
			K	1=2	-	-	1>4*	-	1>3*
			Total	-	-	-	1>4**	-	-
335	0	0	H	-	-	3>4*	1>4*	2>4*	-
			K	1=2	2>3**	3=4	1=4	2>4**	1=3
			Total	-	-	3>4*	1>4**	2>4***	-
370	0	0	K	1=2	2<3***	3>4***	1>4*	2>4**	1<3***
			P	1=2	2>3***	3<4**	1=4	2=4	1>3***
			Total	-	-	-	-	-	-

Table 35 (continued)

Note. LH = left hemisphere; RH = right hemisphere; 0 indicates no damage; 1 = small; 2 = moderate; and 3 = complete damage. Birds 335 and 370 were control animals which sustained damage to areas medial or dorsal to nucleus basalis (NB). Differences indicated refer to preoperative periods 1 and 2 and postoperative periods 3 and 4. Prior analyses of variance computed on the daily intake of each kind of seed and on total intake (1:2:3:4; 1:2:3 and 2:3:4) were significant ($p < .05$, or better) unless indicated (-).

[a] H = hemp, K = kafir, P = peas

* $p < .05$

** $p < .01$

*** $p < .001$

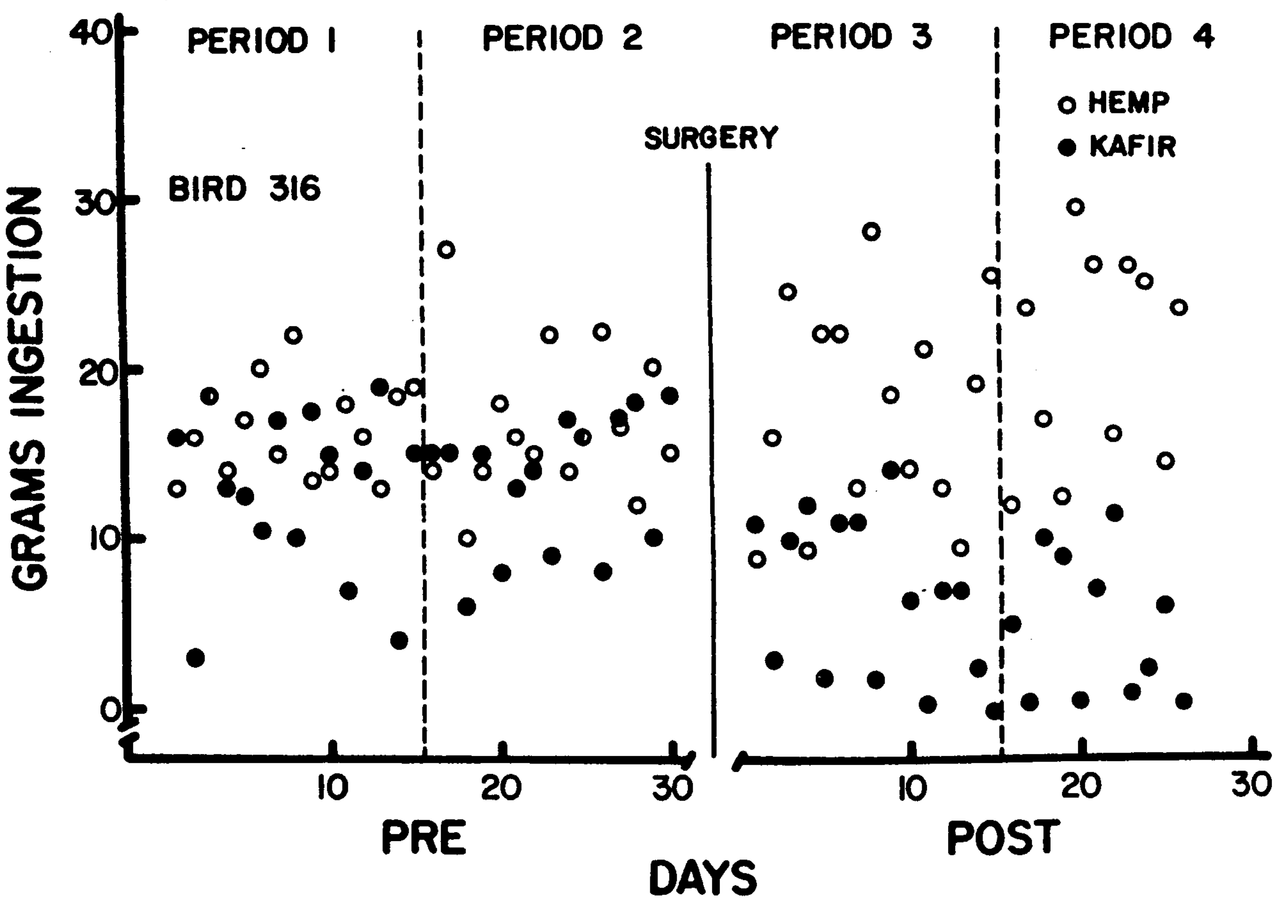


FIG. 21. Seed ingestion(g) by bird 316 pre- and postoperatively. Hemp, kafir and peas were offered ad libitum. Peas were not eaten. Periods 1, 2, and 3 were 15 days each. Period 4 was 11 days. The rating assigned to NB damage was: Left Hemisphere, 2; Right Hemisphere, 2 (See text).

NB damage, this subject was aphagic for two days, and then ate significantly less kafir while maintaining the same level of hemp intake. Bird 329 (Figure 22), which sustained primarily unilateral damage, was not aphagic after surgery but also showed an immediate postoperative decrease in kafir intake. These two birds showed very different patterns of intake in the postoperative period. Bird 329 increased kafir intake throughout period 3 so that its kafir intake in period 4 equalled that of period 2. Bird 316, which sustained a larger bilateral lesion, maintained the same depressed level of kafir intake in periods 3 and 4. Bird 335 (Figure 23), which sustained small bilateral lesions in the areas of N and HvDv, and had no NB damage, also showed an immediate postsurgical decrease in kafir intake. This change is not comparable to that seen for the other subjects, as bird 335 showed a significant increase in kafir intake between periods 1 and 2.

Kafir intake in periods 3 and 4 was not significantly different from that for period 1 (Table CC).

Postoperative Decreases in Kafir Intake and Increases in Hemp Intake. Birds 376 and 382 (Figures 24 and 25), which sustained small to moderate bilateral NB damage also showed immediate postsurgical decreases in kafir intake. In addition, these subjects showed concurrent, and significant, increases in hemp intake

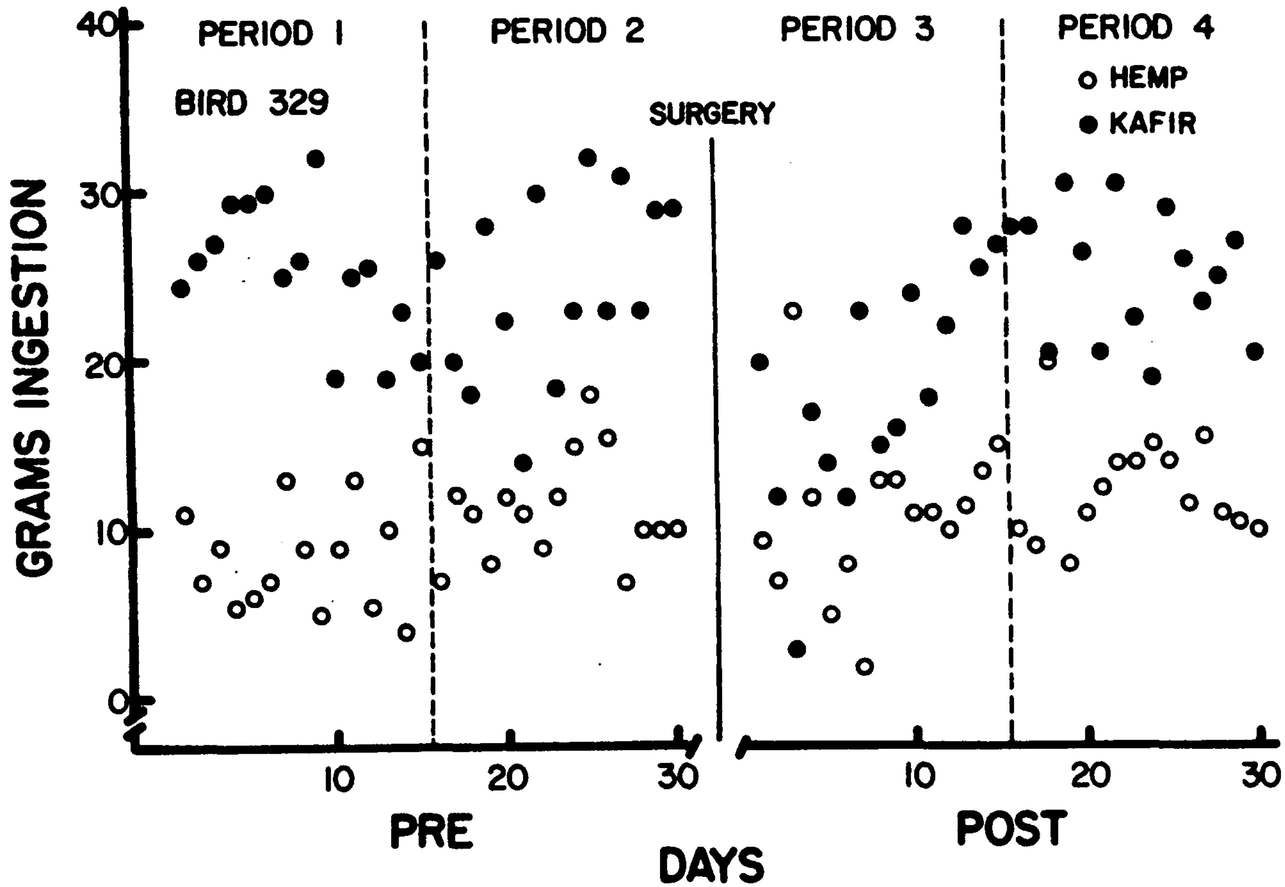


FIG. 22. Seed ingestion(g) by bird 329 pre- and postoperatively. Hemp, kafir and peas were offered <u>ad libitum</u> during 4 consecutive 15-day periods. Peas were not eaten. The rating assigned to NB damage was: Left Hemisphere, 0-1; Right Hemisphere, 2 (See text).

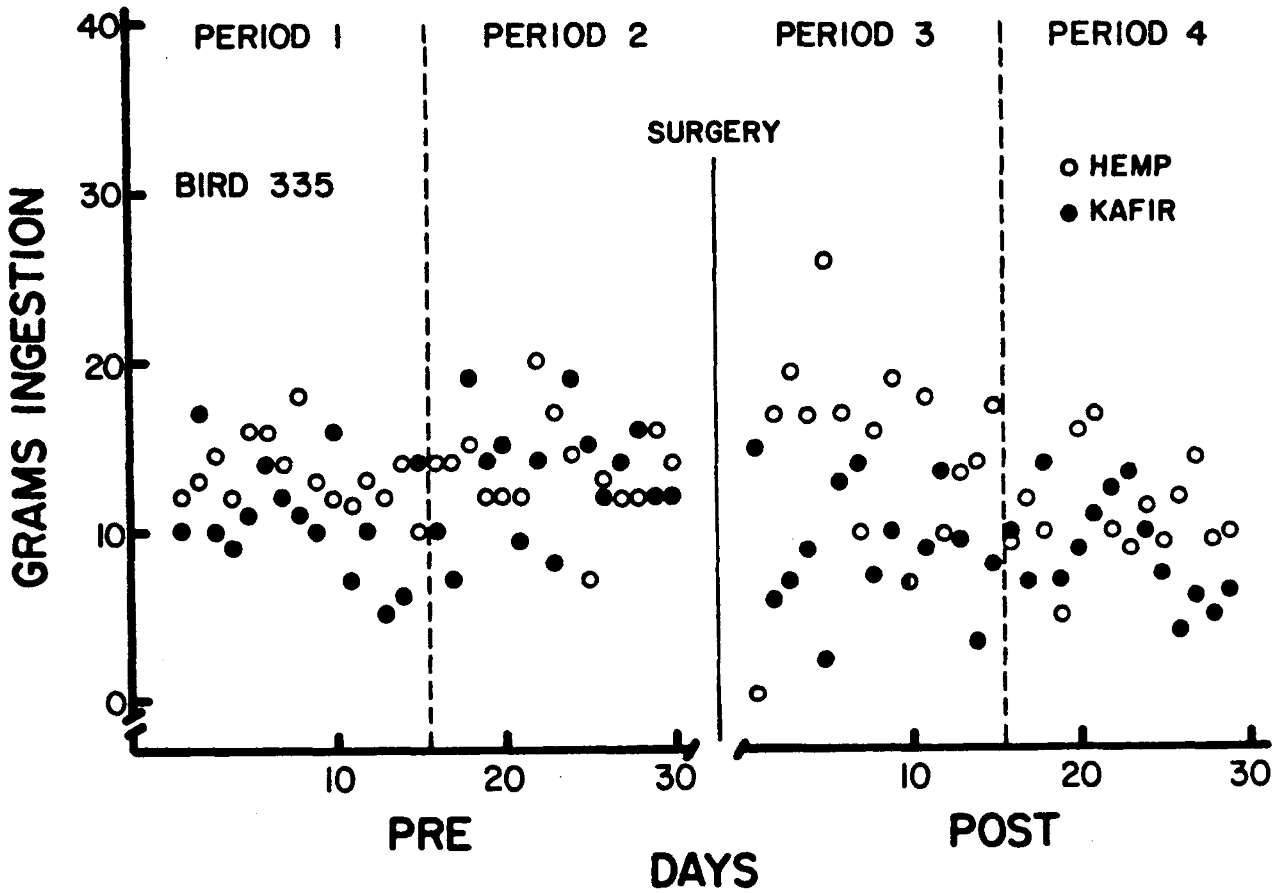


FIG. 23. Seed ingestion(g) by bird 335 pre- and postoperatively. Hemp, kafir, and peas were offered ad libitum. Peas were not eaten. Periods 1, 2, and 3 were 15 days each. Period 4 was 14 days. The rating assigned to NB damage was: Left Hemisphere, 0; Right Hemisphere, 0 (See text).

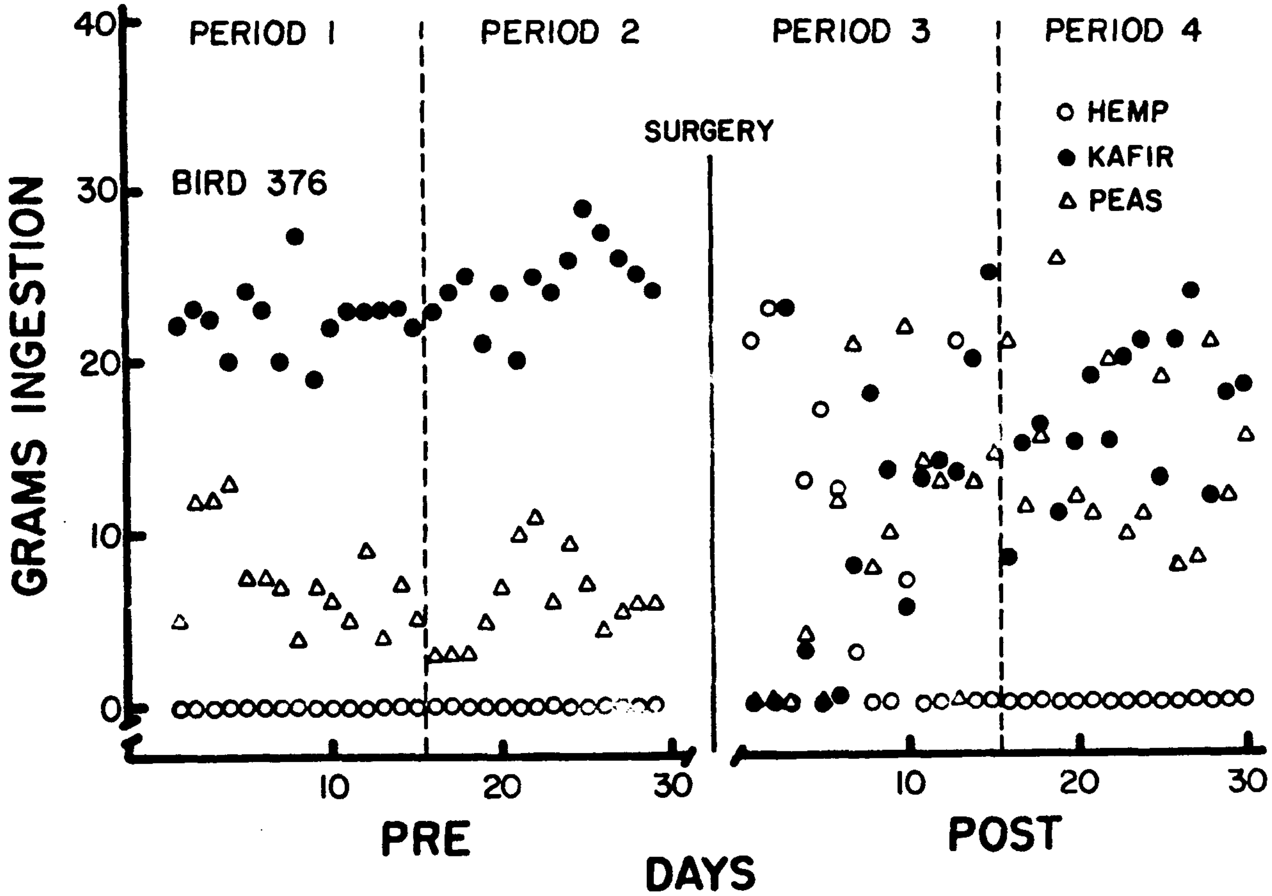


FIG. 24. Seed ingestion(g) by bird 376 pre- and postoperatively. Hemp, kafir, and peas were offered _ad libitum_ in 4 consecutive 15-day periods. The rating assigned to NB damage was: Left Hemisphere, 2-3; Right Hemisphere, 1 (See text).

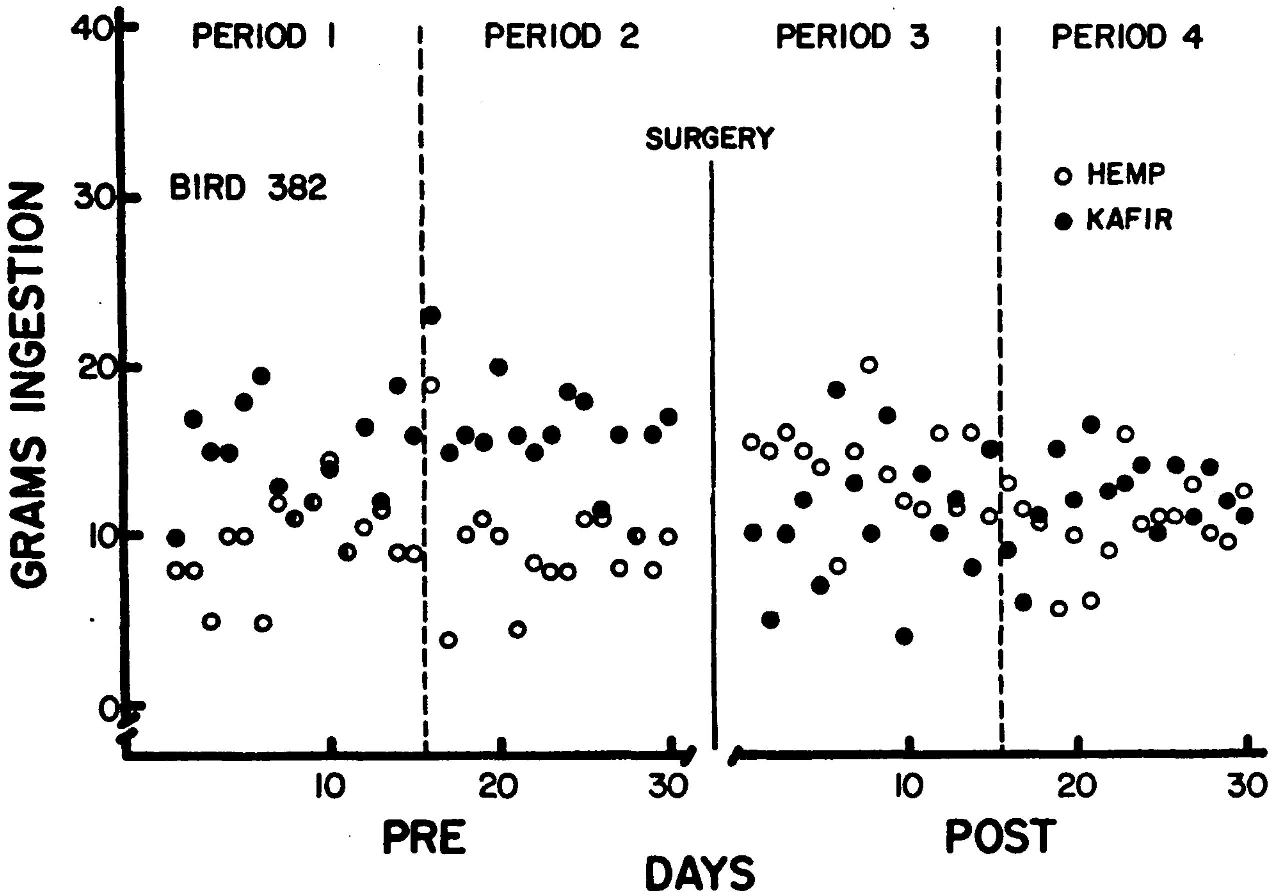


FIG. 25. Seed ingestion(g) by bird 382 pre- and postoperatively. Hemp, kafir, and peas were offered ad libitum during 4 consecutive 15-day periods. Peas were not eaten. The rating assigned to NB damage was: Left Hemisphere, 1; Right Hemisphere, 1-2 (See text).

within period 3. This represents a rather profound and dramatic change for bird 376 which did not eat hemp previously. Hemp intake decreased for both subjects by the fourth period, but kafir intake remained significantly below the period 2 level in both period 3 and period 4.

Postoperative Increases in Hemp Intake. Bird 9 (Figure 26), which sustained moderate unilateral NB damage significantly increased its hemp intake immediately after surgery and then largely reversed this postoperative change before the end of period 3.

Postoperative Increases in Kafir Intake. Bird 370 (Figure 27), which sustained moderately large lesions of LPO but no damage to NB or QFT, was the only subject which showed a postoperative increase in kafir intake. Figure 27 suggests that this change may be secondary to an immediate postsurgical decrease in peas intake: kafir intake returns to its preoperative level when peas are ingested. Unfortunately, direct comparisons with the other subjects which sustained NB damage are hampered by the different diet of bird 370. It should be noted, however, that deafferented subjects in a previous experiment (see section IV A) ate different kinds of seeds with kafir but showed similar decreases in kafir intake. The changes seen for bird 370 in period 3 are gradually reversed so that the seed ingestion in period 4 is similar to that of period 1.

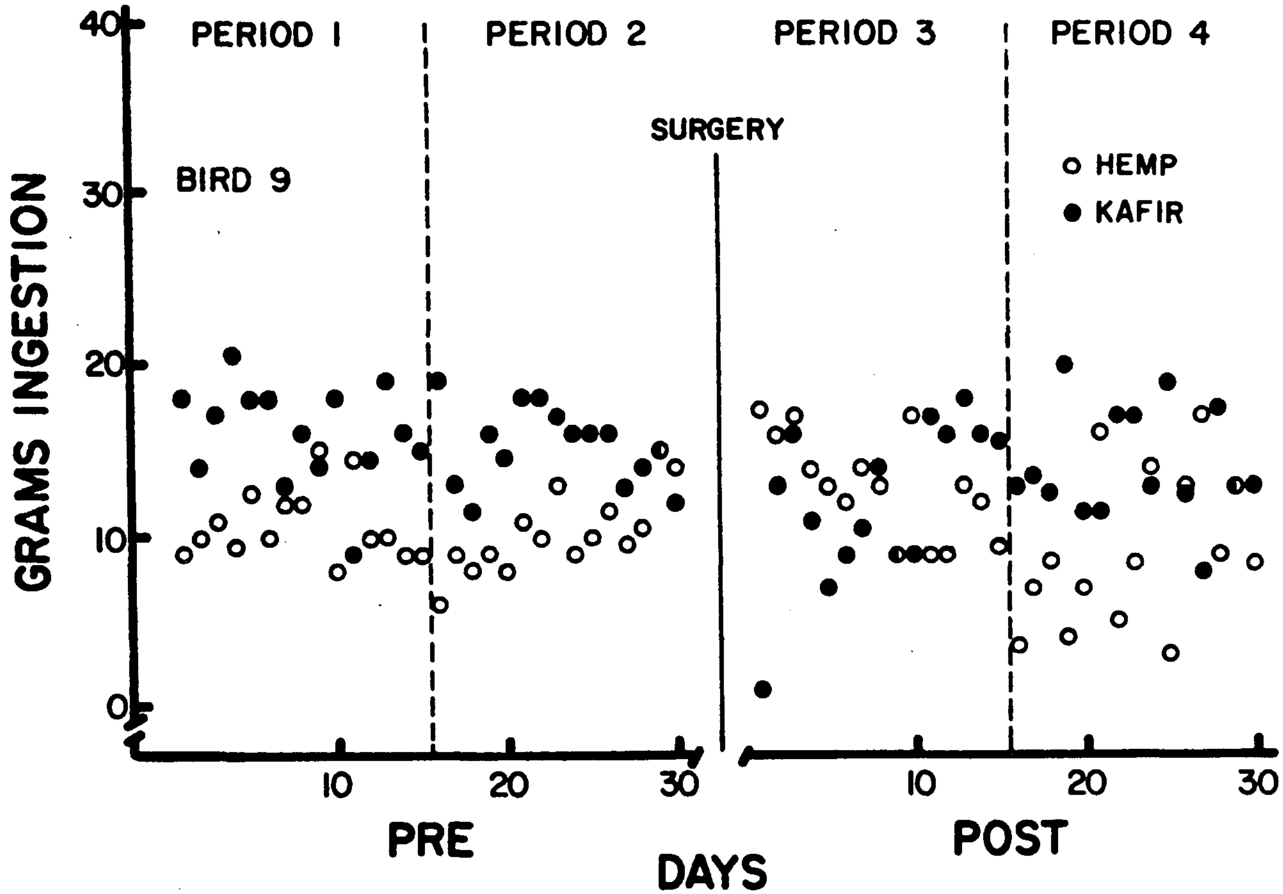


FIG. 26. Seed ingestion(g) by bird 9 pre- and postoperatively. Hemp, kafir, and peas were offered ad libitum during 4 consecutive 15-day periods. Peas were not eaten. The rating assigned to NB damage was: Left Hemisphere, 0; Right Hemisphere, 1 (See text).

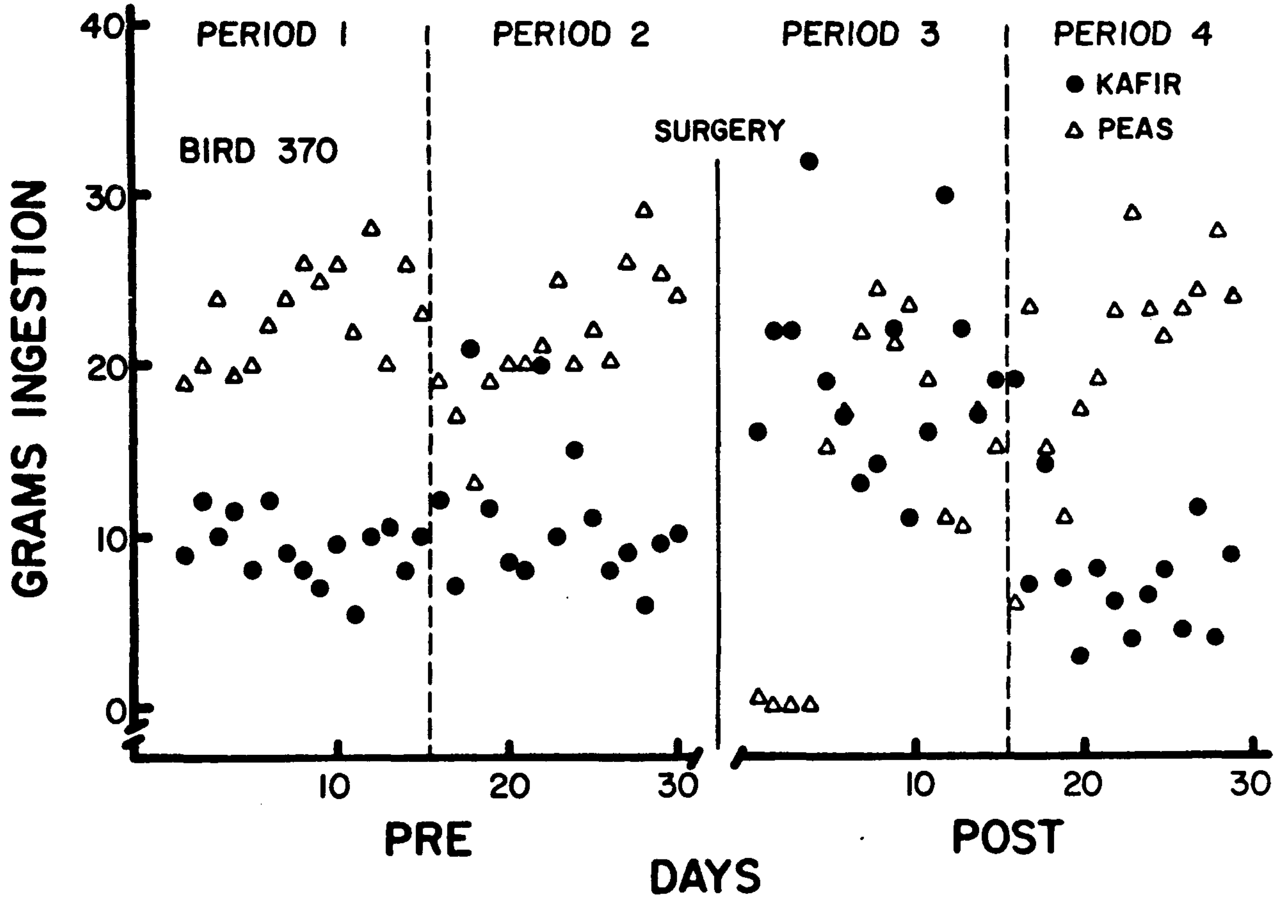


FIG. 27. Seed ingestion(g) by bird 370 pre- and postoperatively. Hemp, kafir, and peas were offered _ad libitum_. Hemp was not eaten. Periods 1, 2, and 3 were 15 days each. Period 4 was 14 days. The rating assigned to NB damage was: Left Hemisphere, 0; Right Hemisphere, 0 (See text).

Changes in Total Food Intake

All subjects showed similar total food intake in periods 1 and 2 and, with the exception of bird 335, in periods 3 and 4 (Table 35). Bird 316, which sustained moderate bilateral NB damage, and bird 329, which sustained primarily unilateral NB damage, ate significantly less food in the third period than in the second. Bird 329 showed a significant, compensatory increase in total food intake in the fourth period while bird 316 did not.

Changes in Water Intake

The data and statistical analyses show water intake was quite variable and that there was no apparent relationship between the loci or size of lesions and changes in water intake (Tables DD and EE).

Changes in Body Weight

The postsurgical response to the body weight lost in surgery and in the immediate postoperative days was quite variable (Tables 36 and 37). Birds 9 and 382, which sustained unilateral and bilateral NB lesions, respectively, and bird 335, which sustained lesions in HV, HvDv, and N (and lost weight before surgery), did not recover their body weight in the fourth period: the period 3 and period 4 weight of these subjects is equal. Birds 316 and 376, which sustained bilateral NB lesions regained some of their lost weight in period 4, but

Table 36

Means and Standard Deviations for Body Weight (g) in 15 Day Periods Before and After Nucleus Basalis Lesions

Bird Numbers	Rating Assigned to NB Damage LH	RH	Pre Period 1 Mean	SD	Pre Period 2 Mean	SD	Post Period 3 Mean	SD	Post Period 4 Mean	SD
316	2	2	695.9	8.1	710.0	2.5	603.6	7.7	612.7	5.4
376	2-3	1	570.6	7.3	560.4	5.0	518.5	7.0	523.4	4.0
382	1	1-2	497.6	6.8	495.4	5.4	483.0	6.7	483.6	5.1
329	0-1	2	642.3	5.2	648.4	8.7	610.5	13.4	631.5	12.8
9	0	1	600.0	6.7	607.7	4.4	587.5	5.7	586.3	4.8
335	0	0	494.9	6.1	477.8	5.8	459.9	9.0	453.0	9.0
370	0	0	604.0	11.4	602.1	6.7	579.7	17.3	599.8	6.8

Note. LH = left hemisphere, RH = right hemisphere, 0 indicates no damage, 1 = small, 2 = moderate and 3 = complete damage. Subjects 335 and 370 were control animals which sustained damage to areas medial or dorsal to nucleus basalis (NB).

Table 37

Mann-Whitney U Tests on Body Weight in 15 Day Periods Before and After Nucleus Basalis Lesions

Bird Numbers	Rating Assigned to NB Damage		Direction of Differences					
	LH	RH	1vs.2	2vs.3	3vs.4	1vs.4	2vs.4	1vs.3
316	2	2	1<2*	2>3***	3<4**	1>4**	2>4**	1>3**
376	2-3	1	-	-	-	-	-	-
382	1	1-2	-	-	-	-	-	-
329	0-1	2	1<2*	2>3**	3<4**	1>4**	2>4*	1>3**
9	0	1	1=2	2>3**	3=4	1>4***	2>4***	1>3**
335	0	0	1>2**	2>3**	3=4	1>4**	2>4**	1>3**
370	0	0	1=2	2>3**	3<4*	1<4*	2=4	1>3***

Note. LH = left hemisphere; RH = right hemisphere; 0 indicates no damage; 1 = small, 2 = moderate; and 3 = complete damage. Birds 335 and 370 were control animals which sustained damage to areas medial or dorsal to nucleus basalis. Differences indicated refer to preoperative periods 1 and 2 and postoperative periods 3 and 4. Prior analyses of variance computed on body weight were significant ($p < .01$, or better) unless indicated (-).

* $p < .05$

** $p < .01$

*** $p < .001$

remained significantly below their period 2 body weight: the period 3 and period 4 body weight of these two subjects is significantly different, reflecting the period 4 weight gain. Birds 329 and 370, which sustained primarily unilateral NB damage, and bilateral LPO damage, respectively, were the only subjects which gained sufficient weight in period 4 to reach their period 1 level of body weight.

Discussion

The surgical results indicated that the birds in this experiment received electrolytic lesions which as a group represented a continuum of damage both with respect to laterality and extent. Bird 316 sustained approximately symmetrical moderate bilateral lesions. Birds 376 and 382 sustained a small NB lesion in one hemisphere and a larger lesion (ratings of 1-2 and 2-3, respectively) in the other hemisphere. Birds 329 and 9 sustained primarily moderate unilateral and small unilateral damage, respectively. Surgical control birds 335 and 370 sustained no NB damage.

Only bird 316 which sustained moderate bilateral damage was aphagic after surgery. Yet all birds which sustained NB damage failed to regain the body weight lost in surgery and during the time (0-5 days) they ate less than 50% of their food intake. Thus, with the exception of birds 376 and 335, NB and control birds which lost weight prior to surgery, and of control bird 370, the unilateral and bilateral lesioned birds were hypophagic: they did not eat sufficient amounts of food to regain their preoperative <u>ad libitum</u> body weight for at least 28 days after surgery. These data confirm that pigeons which show little or no aphagia after NB damage are hypophagic for many weeks

(Zeigler & Karten, 1973a).

Differential Seed Ingestion

The length of time kafir intake remained decreased after surgery appeared to be a function of the size and bilateral extent of the NB lesions. Thus, bird 9 which sustained a small unilateral NB lesion recovered its typical preoperative intake of kafir by the second postsurgical day while bird 316, the only bird to sustain large equivalently bilateral NB lesions had a decreasing kafir intake throughout period 3 which remained depressed during period 4 (cf. Figures 21 and 26). Birds which sustained smaller unilateral NB lesions (e.g., 329 and 9) showed more transient postsurgical decreases in kafir intake. They approached or recovered their typical presurgical levels of kafir intake at different times but before the last several days of period 3. These decreases in kafir intake appear to be directly related to sensorimotor deficits which disrupt mandibulation and decrease the efficiency of feeding (Zeigler & Karten, 1973b). This view is supported by the data for bird 9 which sustained unilateral NB damage and showed a decrease in kafir intake which was not statistically significant; unilateral NB lesions do not lead to decreases in the efficiency of feeding (Zeigler & Karten, 1973b).

The increased hemp intake observed for several birds may reflect a greater relative frequency of reinforcement associated with pecks which are directed toward hemp. However, bird 376, which sustained bilateral NB damage, and rather extensive damage to structures adjacent to NB (including bilateral damage to E, FA, HvDv, HVvv, LPO, and PA) showed changes in the differential ingestion of seeds not explained by the differential reinforcement and/or efficiency hypotheses. Hemp, which was not eaten during the presurgical period was the only seed eaten during the first 4 postsurgical days even though peas had been eaten preoperatively. The amounts of hemp eaten were considerable: during the first two days intake was 10.0 and 10.5 grams, respectively, but was below 50% of the *ad libitum* intake. On the next two days hemp intake was 21 grams and 23 grams, respectively. On the 5th day, 23 grams of kafir were eaten! Hemp intake subsequently decreased to zero while kafir intake increased but remained below the preoperative level. Peas intake then increased in period 3 when compared with the immediate postsurgical period but was not significantly greater than in period 2. However, the intake of peas in period 4 was significantly greater than that seen in period 3 or 2.

It would appear that a decreased efficiency of eating smaller seeds after NB lesions leads to a decreased intake of kafir and to secondary increases in the intake of larger seeds but that substantial damage to structures adjacent to NB may interfere with this typical postsurgical response. In the case of bird 376 a recovery of function(s) apparently preceded the characteristic postsurgical shift to eating small amounts of kafir and, secondarily, greater amounts of larger seeds. Thus, the apparent responses to seed size, seen immediately after surgery in several one- and two-branch birds (above, See Section IVA) and in other birds with primarily unilateral (329) or with bilateral NB lesions, was not seen until period 4 in the case of bird 376. Thus, the apparent delayed responsiveness to the differential efficacy of eating several kinds of seeds could be an anomaly associated with this bird's decreased, preoperative body weight. However, data presented above (Section IIID) shows that body weight loss per se does not alter the differential ingestion of seeds in this manner. Furthermore, data from a recent study suggests that birds which sustain body weight loss prior to peripheral trigeminal damage may show a more nearly typical responsiveness to food than birds lesioned at their *ad libitum* body weight (Zeigler, 1974a).

The changes in seed ingestion observed after unilateral and bilateral NB damage appear quite similar to those observed after one- and two-branch deafferention. The similarity and differences between "peripheral" and "central" trigeminal lesions are presented below in the General Discussion.

V

General Discussion

These studies were conducted to determine the feasibility of using the pigeon's differential ingestion of seeds as a dependent variable to assess the effects of trigeminal lesions on feeding behavior. They showed that pigeons manifest a significant differential ingestion of seeds which varies from day to day but is more variable for some birds than for other birds. The degree of variability observed appeared to be independent of the number and kinds of seeds offered and the methods of presentation employed. However, while the daily intake of particular seeds varied within and between birds each bird generally ate the same kinds of seeds during a 30 day observation period. The differential ingestion of seeds was transsituational and even periods of eating only a single kind of food were not sufficient to reliably induce changes in seed ingestion.

Body weight loss following food deprivation, however, did alter the ingestion of seeds observed when one compared the ingestion of the same birds under *ad libitum* and food deprived conditions. Birds reduced to 90%, 80%, or 70% of their *ad libitum* body weight were likely to decrease the percentage of large seeds eaten and increase the intake of small seeds. Peripheral and central trigeminal lesions led to an aphagia and hypophagia which also resulted in body weight loss. However, upon the recovery of feeding after trigeminal lesions, there was an immediate or progressive decline in the intake of small seeds and an immediate and frequently maintained increased ingestion of large seeds. These postsurgical changes in seed ingestion were fairly stable whether one- or two-branch peripheral lesions were sustained. In the case of nucleus basalis (NB) damage, however, the effects depended on the bilateral extent of the lesions. After small or primarily unilateral NB lesions, the preoperative seed ingestion recovered within a two week period. Large symmetrical bilateral NB lesions, which also impinged upon adjacent areas, resulted in a complete disruption of the preoperative seed ingestion. Only after a period of time did a bird which sustained rather extensive lesions show the characteristic pattern of peripherally deafferented birds and birds which sustained small bilateral or unilateral NB lesions, that is, a decreased ingestion of small seeds and an increased ingestion of large seeds.

Consideration of Mechanisms Which Might Lead to a Change in the Ingestion of Seeds After Trigeminal Lesions

The postsurgical aphagia and hypophagia observed after trigeminal lesions leads to increased hunger operationally defined as percent body weight loss. This weight loss could affect the ingestion of seeds in several different ways. Body weight loss changes the pigeon's pattern of feeding (Zeigler, et. al., 1971) and "preference" for certain colors (Delius, 1971). In other species, hunger has been shown to change the responsiveness to specific items in a diet (e.g., Holling, 1965) and increase the force of pecking (Feekes, 1971). The levels of hunger, patterns of feeding, pecking force and kinds of ingestants would appear to be interrelated.

In this study the seed ingestion observed in ad libitum feeding after body weight loss differed with the method used to bring about weight loss. Therefore, body weight loss or "hunger" in this instance is, in and of itself, not sufficient to explicate the processes underlying the changes in differential seed ingestion seen after trigeminal lesions. These results are consistent with a previous study suggesting that increases in the pigeon's general responsiveness to foods may not be associated with increases in the pigeon's responsiveness to specific seeds (See Brown, 1969).

It has been suggested that the trigeminal lesioned bird's aphagia could be due to "pain" of the oral region or beak. If this were true, the pigeon could reject foods previously eaten because they became conditioned stimuli (CS) associated with "pain", unconditioned stimuli (UCS), during initial postoperative attempts to eat. This conditioning would presumably result in an aversion analogous to that shown for deficient diets (Rozin & Kalat, 1971). However, there would appear to be at least one problem with this explanation for the observed changes in seed ingestion: it does not suggest how one kind of seed becomes aversive while other seeds do not become aversive. One would have to assume, it appears, that a lesioned bird only pecks at kafir immediately after surgery and that eating then ceases for a period so that only kafir becomes aversive. However, the data show that many birds eat some of each of the different kinds of seeds after surgery. It would seem that "pain" would be associated with all of the seeds eaten. There is no reason to believe that the characteristics of any one of the kinds of seeds offered would provide the effective aversive stimulus (UCS) which could lead to only its rejection.

"Pain" could, perhaps, be restricted to specific sensory fields within the inner beak or palate, which are subserved by NB, on the one hand, or by the Gasserian ganglion in the case of the trigeminal sensory branches. It is not unreasonable that seeds of different size could selectively impinge upon different sensory fields and that only small seeds which intimately contact the sensory fields of the soft tissues in the inner beak would provide aversive stimulation. As pigeons which have been subjected to deafferentation or NB lesions peck at an operant key and drink normally, "pain" has been largely excluded as a basis for the aphagia observed after trigeminal damage. However, if the contact of small grains within the buccal cavity resulted in "pain", operant pecks at a key with the tip of the beak might not necessarily provide a comparably "painful" UCS. If small seeds did produce aversive stimulation they might only be picked up and then dropped even though they were previously eaten in large amounts. Other seeds which were previously not eaten but which did not impinge upon the "painful" sensory fields due to their larger size, might be ingested. The evidence presented below suggests "pain" is not the cause of the observed changes in seed ingestion, however, further research would be required to adequately test this hypothesis.

It has also been suggested that changes in seed ingestion observed after trigeminal damage could reflect an inability to discriminate seeds or an inability to ingest seeds on the basis of previous conditioned associations between the seeds' orotactual and visual characteristics and their postingestional qualities. It has been hypothesized that "trigeminal stimuli" may be relatively more important in the control of the pigeon's feeding than olfaction and taste (Zeigler & Karten, 1973). Thus, it might be expected that the orotactile sense subserved by the trigeminal sensory nerves would provide the primary sensory basis for the orovisual conditioning which has been shown to underlie the formation of characteristic feeding habits. The lesions in the present study provided a direct test of the degree to which an unimpaired orotactile sense was requisite for those discriminations of food quality which provide the basis for a differential ingestion of seeds. However, the primary changes observed did not seem related to a deficit in the discrimination of seeds which was directly attributable to an impaired orotactile sense. There were significantly different numbers of seeds ingested and presumably different numbers of pecks directed toward the several different seeds offered even when the grams intake of each seed was similar. Thus, an equal grams ingestion of seeds which might suggest a discrimination deficit is, in fact, the result of eating many small seeds and fewer large seeds. Even when the ingestion of seeds was directly related to seed size, the number of seeds ingested were significantly different. Thus, the data did not show a discrimination deficit or suggest the conditioning of new associations between UCS associated with the postingestional effects of seeds and new postsurgical CS associated with an impaired orotactile sense.

Comparisons of Peripheral Deafferentation and Central Electrolytic Lesions of Trigeminal Neural Structures

The roles that the peripheral trigeminal sensory branches and NB may have in the orosensory control of food intake is suggested by the several electrophysiological studies which recorded unit responses to tactile stimulation of the buccal cavity and beak. Single unit recordings from cells whose elements form the trigeminal sensory branches, and which are afferent to the main sensory trigeminal nucleus (PrV) showed that these cells respond to sustained light touch of the beak and buccal cavity and inhibit spontaneous firing when the beak is opened and closed (manually). Comparisons of the response characteristics of single units within PrV and NB indicate the cells within these nuclei may serve different but complementary functions which might be revealed with sensitive behavioral measures. This functional specificity could account for the different postsurgical response to hemp and kafir. The overlap of the sensory fields subserved by these trigeminal structures could provide a basis for the recovery of sensory deficits. However, the degeneration and regeneration of the pigeon's trigeminal nerves has not been sufficiently investigated to be certain that anterograde and retrograde degeneration does not make the designations "peripheral" and "central" misleading or meaningless.

While comparisons of "central" and "peripheral" trigeminal damage are not possible until studies of degeneration have been conducted the data suggest: (1) both peripheral and central trigeminal lesions led to prolonged periods of hypophagia despite the high probability that the birds were capable of ingesting sufficient amounts of large seeds to regain their lost body weight, (2) both peripheral and central lesions change seed ingestion in a manner which would appear to be explained primarily on the basis of lesion induced sensorimotor deficits, (3) central trigeminal lesions inevitably involve damage to adjacent neural structures which in some cases appears to delay the characteristic decreased ingestion of small seeds and increased ingestion of large seeds seen immediately after effective one- and two-branch lesions, (4) the trigeminal orotactile sense is necessary but not sufficient for the pigeon's differential ingestion of seeds.

APPENDIX

Table A

Means, Standard Deviations(SD), and Coefficients of Variation(CV) for Daily Food and Water Intake(g) and for Body Weight(g) of Birds Given Two Grain Presentations

Bird Numbers	FOOD INTAKE			WATER INTAKE			BODY WEIGHT		
	MEAN	SD	CV	MEAN	SD	CV	MEAN	SD	CV
310	36.2	3.7	10.0	128.5	30.5	24	606.2	7.1	1.2
395	26.5	6.7	25.0	45.4	12.1	27	564.8	6.5	1.2
398	29.1	4.8	17.0	53.8	9.4	17	553.8	5.9	1.1
405	28.6	2.7	10.0	90.2	81.4	90	570.4	4.3	0.8
411	41.3	2.7	0.1	85.9	10.4	12	663.6	8.2	1.2

Table B

Means, Standard Deviations(SD), and Coefficients of Variation(CV) for Daily Food and Water Intake(g) and for Body Weight(g) of Birds Given Three Grain Presentations

Bird Numbers	FOOD INTAKE			WATER INTAKE			BODY WEIGHT		
	MEAN	SD	CV	MEAN	SD	CV	MEAN	SD	CV
9	25.0	3.2	13.0	151.9	32.1	21.0	602.2	6.5	1.0
13	21.9	4.2	19.0	45.9	9.8	21.0	560.1	5.3	1.0
20	26.8	4.6	17.0	118.8	29.6	25.0	583.6	11.6	2.0
28	28.5	5.9	21.0	126.3	30.8	24.0	616.4	5.7	1.0
316	29.3	5.4	18.0	138.3	33.4	24.0	702.5	9.5	1.0
329	32.2	4.6	16.0	70.3	29.0	41.0	647.1	8.4	1.0
333	25.2	3.0	12.0	67.9	26.7	39.0	547.8	9.6	2.0
335	25.8	4.2	16.0	118.6	28.6	24.0	491.0	8.4	2.0
341	27.1	7.3	27.0	45.9	14.6	32.0	550.9	9.3	2.0
354	25.6	3.2	13.0	55.4	11.0	20.0	567.0	6.4	1.0
365	24.8	3.0	12.0	48.4	19.0	39.0	636.6	3.2	0.5
369	29.1	3.3	11.0	46.7	7.3	16.0	646.7	3.1	0.5
370	29.2	4.9	17.0	46.9	9.4	20.0	600.9	9.6	1.6
376	29.3	3.3	11.0	86.5	40.7	47.0	566.5	7.8	1.4
377	23.9	5.2	22.0	61.2	11.2	18.0	565.9	7.5	1.3
381	30.8	4.2	14.0	141.3	27.8	20.0	742.7	6.7	0.9
382	25.0	4.9	20.0	69.8	15.1	22.0	497.6	6.2	1.3
507	38.8	3.7	15.0	76.6	14.8	19.0	629.0	11.6	1.9
526	38.8	3.7	0.1	148.5	24.1	16.0	592.6	10.6	1.8

Table C

Means, Standard Deviations(SD), and Coefficients of Variation(CV) for Daily Food and Water Intake(g) and for Body Weight(g) of Birds Given Four Grain Presentations

Bird Numbers	FOOD INTAKE			WATER INTAKE			BODY WEIGHT		
	MEAN	SD	CV	MEAN	SD	CV	MEAN	SD	CV
306	29.4	5.1	17	53.5	12.0	22	557.5	10.0	1.8
392	24.4	5.1	21	42.1	11.2	27	492.9	7.4	1.5
393	28.2	3.9	14	34.5	5.0	15	681.3	11.2	1.7
394	30.6	3.4	11	60.2	9.9	16	589.4	6.8	1.2

Table D

Interrelationships Between Mean Food Intake(g) and Mean Body Weight(g) During Two Grain Presentations

Bird Numbers	W/F	W/BW	F/BW	RHO-F:W
310	3.55	.21	.06	.69
395	1.71	.08	.05	.92
398	1.85	.10	.05	.95
405	3.15	.16	.05	.77
411	2.08	.13	.06	.83

Note. W=water, F=food, BW=body weight, RHO=rank order correlation coefficient for daily grams food: daily grams water over 30 days

Table E

Interrelationships Between Mean Food Intake(g) and Mean Body Weight(g) During Three Grain Presentations

Bird Numbers	W/F	W/BW	F/BW	RHO-F:W
9	6.08	.25	.04	.91
13	2.10	.08	.04	.71
20	4.43	.20	.05	.61
28	4.43	.21	.05	.83
316	4.72	.20	.04	.81
329	2.18	.12	.05	.87
333	2.69	.12	.05	.73
335	4.60	.24	.05	.91
341	1.70	.08	.05	.76
354	2.16	.10	.05	.76
365	1.95	.08	.04	.75
369	1.61	.07	.05	.83
370	1.61	.08	.05	.93
376	2.95	.15	.05	.81
377	2.56	.12	.04	.93
381	4.59	.19	.04	.90
382	2.79	.14	.05	.82
507	2.15	.12	.06	.74
526	3.83	.25	.07	.84

Note. W=water, F=food, BW=body weight, RHO=rank order correlation coefficient for daily grams food: daily grams water over 30 days

Table F

Interrelationships Between Mean Food Intake(g) and Mean Body Weight(g) During Four Grain Presentations

Bird Numbers	W/F	W/BW	F/BW	RHO-F:W
306	1.82	.10	.05	.77
392	1.73	.09	.05	.97
393	1.23	.05	.04	.74
394	1.97	.10	.05	.83

Note. W=water, F=food, BW=body weight, RHO=rank order correlation coefficient for daily grams food: daily grams water over 30 days

Table G

Means and Standard Deviations for Water Intake (g) During Paired (PG) and Three Grain (3G) Presentations

Bird Numbers	PG Mean	PG SD	3G Mean	3G SD
Group 3GPG				
344	118.7	38.3	222.4	46.4
346	121.4	22.9	120.1	12.7
515	68.4	11.7	67.5	10.0
530	63.1	8.0	62.0	9.9
Group PG3G				
337	110.0	23.8	137.0	23.9
366	92.3	25.7	132.0	22.8
508	174.4	34.4	233.6	33.7
510	236.7	18.2	215.3	41.6
527	81.2	37.6	72.6	12.7
534	87.8	11.6	107.9	14.9

Table H

Means and Standard Deviations for Body Weight (g) During Paired (PG) and Three Grain (3G) Presentations

Bird Numbers	PG Mean	PG SD	3G Mean	3G SD
Group 3GPG				
344	617.0	5.9	621.5	5.8
346	617.0	18.4	616.0	18.1
515	500.0	4.0	497.5	13.8
530	505.0	4.4	505.5	5.0
Group PG3G				
337	620.0	5.7	617.0	5.4
366	578.0	13.8	598.0	11.0
508	556.0	3.7	522.0	8.6
510	592.0	8.6	594.0	7.6
527	608.0	5.2	624.0	6.1
534	520.0	1.9	526.0	3.2

Table I

Mann-Whitney U Tests on Total Food and Water Intake and Body Weight During the Pre-Restriction, Restriction, and Postrestriction Periods

Bird Numbers	Restricted[a] Seed	Total Food Intake			Water Intake			Body Weight		
		1:3	1:2	2:3	1:3	1:2	2:3	1:3	1:2	2:3
					Experimentally Naive Birds					
511	Hemp(28.5)	ns	***1>2	***2<3	--	--	--	--	--	--
514	Hemp(24.8)	ns	***1>2	***2<3	--	--	--	--	--	--
321	Hemp(0)	ns	***1>2	***2<3	ns	***1>2	***2<3	*1>3	**1>2	ns
327	Kafir(40.0)	ns	***1>2	***2<3	ns	**1>2	***2<3	ns	*1>2	**2<3
					Birds Previously Offered Hemp, Kafir and Peas					
344	Kafir(32.5)	ns	***1>2	ns	--	--	--	***1>3	**1>2	*2<3
530	Kafir(29.3)	*1>3	***1>2	*2<3	ns	*1>2	*2>3	**1>3	**1>2	ns
515	Kafir(19.0)	ns	***1>2	***2<3	***1<3	**1>2	***2<3	**1>3	**1>2	*2<3

Note. Prior analyses of variance computed on food and water intake and body weight (1:2:3) were significant ($p < .05$ or better) except where indicated (-) for birds 511, 514, and 344. 1, 2, and 3 indicate the prerestriction, restriction, and postrestriction periods, respectively.

[a]The numbers in parentheses are the median daily total intake(g) during the restriction period.

*$p < .05$
**$p < .01$
***$p < .001$

Table J

Means and Standard Deviations for Water Intake(g) During the Pre-Restriction, Restriction, and Postrestriction Periods

Bird Numbers	Restricted Seed[a]	Pre Restriction Mean	Pre Restriction SD	Restriction Mean	Restriction SD	Post Restriction Mean	Post Restriction SD
		Experimentally Naive Birds					
511	Hemp(28.5)	116.3	45.7	114.9	9.3	125.3	23.2
514	Hemp(24.8)	92.2	16.8	100.7	19.5	90.4	16.1
321	Hemp(0)	57.2	11.9	21.7	9.1	49.4	11.4
327	Kafir(40.0)	181.2	27.4	119.3	41.8	194.7	45.7
	Birds Previously Offered Hemp, Kafir and Peas						
344	Kafir(32.5)	172.8	39.2	166.0	20.3	149.9	33.2
530	Kafir(29.3)	73.7	11.4	63.2	18.9	86.8	33.1
515	Kafir(19.0)	73.2	15.9	44.7	18.6	89.3	12.2

[a]The numbers in parentheses are the median daily food intake(g) during the restriction period.

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Table K

Means and Standard Deviations for Body Weight(g) During the Prerestriction, Restriction, and Postrestriction Periods

Bird Numbers	Restricted Seed[a]	Pre Restriction Mean	Pre Restriction SD	Restriction Mean	Restriction SD	Post Restriction Mean	Post Restriction SD
Experimentally Naive Birds							
511	Hemp(28.5)	699.8	11.8	691.0	8.8	688.3	7.8
514	Hemp(24.8)	511.8	4.6	513.0	5.6	510.7	2.2
321	Hemp(0)	584.3	12.7	524.3	35.5	550.8	19.2
327	Kafir(40.0)	628.7	7.6	609.7	11.4	635.3	9.1
Birds Previously Offered Hemp, Kafir and Peas							
344	Kafir(32.5)	624.0	8.1	597.2	7.9	606.0	4.7
530	Kafir(29.3)	507.2	4.7	494.8	6.4	494.8	4.3
515	Kafir(19.0)	514.7	5.7	473.8	19.0	499.3	4.5

[a]The numbers in parentheses are the median daily food intake(g) during the restriction period.

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Table L

Seed Ingestion of Bird 337 in Feeding Periods After Body Weight Loss

PERCENT BODY WEIGHT LOSS		GRAMS Hemp	Kafir	Peas	Total	PERCENT Hemp	Kafir	Peas
0%		13.3	6.8	19.3	40.5	34.6	24.0	44.7
10%	5m	0.0	9.0	16.0	25.0	0.0	36.0	64.0
	5m	6.5	3.0	3.0	12.5	52.0	24.0	24.0
	5m	3.0	6.0	1.5	10.5	28.5	57.1	14.2
	15m	7.5	2.5	0.5	10.5	71.4	23.8	4.7
	15m	2.5	2.0	0.5	5.0	50.0	40.0	10.0
	15m	1.5	0.5	0.0	2.0	75.0	25.0	0.0
	23hrs	6.0	1.5	1.5	9.0	66.6	16.6	16.6
	24hrs	27.0	24.5	23.0	74.5	36.2	32.8	30.8
20%	5m	9.0	1.5	15.0	25.5	35.2	5.8	58.8
	5m	3.0	9.0	0.5	12.5	24.0	72.0	4.0
	5m	7.0	4.5	0.0	11.5	60.8	39.1	0.0
	15m	5.0	6.0	1.0	12.0	41.6	50.0	8.3
	15m	0.0	2.5	0.0	2.5	0.0	100.0	0.0
	15m	2.5	5.5	0.0	8.0	31.2	68.7	0.0
	23hrs	9.0	5.5	4.0	18.5	48.6	29.7	21.6
	24hrs	35.5	34.5	20.5	90.5	39.2	38.1	22.6
30%	5m	4.5	7.5	14.0	26.0	17.3	28.8	53.8
	5m	4.0	9.5	0.5	14.0	28.5	67.8	3.5
	5m	5.5	5.0	0.0	10.5	52.3	47.6	0.0
	15m	12.0	1.5	0.0	13.5	88.8	11.1	0.0
	15m	0.0	6.0	0.0	6.0	0.0	100.0	0.0
	15m	1.0	6.5	0.0	7.5	13.3	86.6	0.0
	23hrs	4.0	6.0	2.5	12.5	32.0	48.0	20.0
	24hrs	31.0	42.0	17.0	90.0	34.4	46.6	18.8

Table M

Seed Ingestion of Bird 366 in Feeding Periods After Body Weight Loss

PERCENT BODY WEIGHT LOSS		GRAMS				PERCENT		
		Hemp	Kafir	Peas	Total	Hemp	Kafir	Peas
0%		27.8	3.3	2.5	35.8	83.9	9.9	6.1
10%	5m	10.0	0.0	0.0	10.0	100.0	0.0	0.0
	5m	2.0	0.5	1.5	4.0	50.0	12.5	37.5
	5m	0.0	1.5	0.0	1.5	0.0	100.0	0.0
	15m	3.5	1.0	0.0	4.5	77.7	22.2	0.0
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	23hrs	21.0	3.5	1.0	25.5	82.3	13.7	3.9
	24hrs	36.5	6.5	2.5	45.5	83.9	10.3	5.7
20%	5m	5.5	0.5	0.5	6.5	84.6	7.6	7.6
	5m	10.0	0.0	0.0	10.0	100.0	0.0	0.0
	5m	3.0	0.0	0.0	3.0	100.0	0.0	0.0
	15m	10.5	3.5	0.0	14.0	75.0	25.0	0.0
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	23hrs	12.0	1.5	0.0	13.5	88.8	11.1	0.0
	24hrs	41.0	5.5	0.5	47.0	87.2	11.7	1.0
30%	5m	11.0	0.0	2.0	13.0	84.6	0.0	15.3
	5m	7.0	0.0	0.0	7.0	100.0	0.0	0.0
	5m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	15m	6.5	1.0	0.0	7.5	86.6	13.3	0.0
	15m	2.0	0.5	0.0	2.5	80.0	20.0	0.0
	15m	3.5	0.5	0.0	4.0	87.5	12.5	0.0
	23hrs	12.5	6.0	1.5	20.0	62.5	30.0	7.5
	24hrs	42.5	8.0	3.5	54.0	78.7	14.8	6.4

Table N

Seed Ingestion of Bird 508 in Feeding Periods After Body Weight Loss

PERCENT BODY WEIGHT LOSS		GRAMS				PERCENT		
		Hemp	Kafir	Peas	Total	Hemp	Kafir	Peas
0%		3.1	2.8	26.3	32.8	10.5	8.8	81.9
10%	5m	0.0	4.0	14.5	18.5	0.0	21.6	78.4
	5m	0.0	1.0	0.0	1.0	0.0	100.0	0.0
	5m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	23hrs	4.0	4.0	6.0	14.0	28.6	28.6	42.8
	24hrs	4.0	9.0	20.5	33.5	12.0	26.8	61.2
20%	5m	4.0	0.0	38.0	42.0	9.5	0.0	90.5
	5m	2.5	2.0	1.0	5.5	45.4	36.4	18.2
	5m	0.0	1.5	0.0	1.5	0.0	100.0	0.0
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	23hrs	1.5	3.0	1.0	5.5	27.3	54.5	18.2
	24hrs	8.0	6.5	40.0	54.5	14.7	11.9	73.4
30%	5m	5.0	0.0	35.5	40.5	12.3	0.0	87.6
	5m	4.0	5.5	1.0	10.5	38.1	52.4	9.5
	5m	1.0	1.5	0.0	2.5	40.0	60.0	0.0
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	23hrs	2.0	8.0	.5	10.5	19.0	76.2	4.8
	24hrs	12.0	15.0	37.0	64.0	18.8	23.4	57.8

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Table O

Seed Ingestion of Bird 510 in Feeding Periods After Body Weight Loss

PERCENT BODY WEIGHT LOSS		GRAMS				PERCENT		
		Hemp	Kafir	Peas	Total	Hemp	Kafir	Peas
0%		15.8	13.0	15.0	43.8	37.5	24.4	36.7
10%	5m	2.0	8.0	11.5	21.5	9.3	37.2	53.5
	5m	3.0	1.0	0.0	4.0	75.0	25.0	0.0
	5m	0.5	1.0	0.0	1.5	33.3	66.7	0.0
	15m	1.0	1.0	0.0	2.0	50.0	50.0	0.0
	15m	1.0	0.0	0.0	1.0	100.0	0.0	0.0
	15m	0.5	0.0	0.0	0.5	100.0	0.0	0.0
	23hrs	6.5	1.5	1.0	9.0	72.0	11.0	17.0
	24hrs	14.5	12.5	12.5	39.5	36.7	31.6	31.6
20%	5m	6.0	7.5	6.5	20.0	30.0	37.5	32.5
	5m	6.0	4.0	0.0	10.0	60.0	40.0	0.0
	5m	0.0	4.0	0.0	4.0	0.0	100.0	0.0
	15m	0.0	4.0	0.0	4.0	0.0	100.0	0.0
	15m	0.0	2.0	1.0	3.0	0.0	66.7	33.3
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	23hrs	13.0	4.0	1.0	18.0	72.2	22.2	5.6
	24hrs	25.0	25.5	8.5	59.0	42.4	43.2	14.4
30%	5m	3.0	10.0	10.0	23.0	13.0	43.5	43.5
	5m	8.0	2.5	0.0	10.5	76.2	23.8	0.0
	5m	4.5	0.0	0.0	4.5	100.0	0.0	0.0
	15m	1.5	1.5	0.0	3.0	50.0	50.0	0.0
	15m	5.0	0.0	0.0	5.0	100.0	0.0	0.0
	15m	1.0	0.0	0.0	1.0	100.0	0.0	0.0
	23hrs	20.0	6.0	0.0	26.0	76.9	23.1	0.0
	24hrs	43.0	20.0	10.0	73.0	58.9	27.4	13.7

Table P

Seed Ingestion of Bird 527 in Feeding Periods After Body Weight Loss

PERCENT BODY WEIGHT LOSS		GRAMS				PERCENT		
		Hemp	Kafir	Peas	Total	Hemp	Kafir	Peas
0%		15.0	6.5	9.8	30.5	50.8	20.9	30.6
10%	5m	11.0	0.0	13.0	24.0	45.8	0.0	54.1
	5m	5.0	2.5	0.0	7.5	66.7	33.3	0.0
	5m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	15m	4.0	1.5	0.0	5.5	72.7	27.2	0.0
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	23hrs	5.5	5.5	1.0	12.0	45.8	45.8	8.3
	24hrs	25.5	9.5	14.0	49.0	52.0	19.3	28.5
20%	5m	8.0	9.0	10.5	27.5	29.0	32.7	38.1
	5m	13.5	2.5	0.5	16.5	81.8	15.1	3.0
	5m	6.5	5.0	0.0	11.5	56.5	43.4	0.0
	15m	6.0	1.0	0.0	7.0	85.7	14.2	0.0
	15m	2.5	4.0	0.0	6.5	38.4	61.5	0.0
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	23hrs	0.5	3.0	1.0	4.5	11.1	66.6	22.2
	24hrs	37.0	24.5	12.0	73.5	63.0	33.6	3.2
30%	5m	12.5	5.5	3.5	21.5	58.1	25.5	16.2
	5m	9.5	4.0	0.0	13.5	70.3	29.6	0.0
	5m	2.5	2.5	0.0	5.0	50.0	50.0	0.0
	15m	7.0	2.0	0.0	9.0	77.7	22.2	0.0
	15m	3.0	2.0	0.0	5.0	60.0	40.0	0.0
	15m	1.0	2.0	0.0	3.0	33.3	66.7	0.0
	23hrs	13.0	10.0	1.0	24.0	54.1	41.6	4.1
	24hrs	48.5	28.0	4.5	81.0	59.8	34.5	5.5

Table Q

Seed Ingestion of Bird 534 in Feeding Periods After Body Weight Loss

PERCENT BODY WEIGHT LOSS		GRAMS				PERCENT		
		Hemp	Kafir	Peas	Total	Hemp	Kafir	Peas
0%		5.3	7.8	19.3	33.5	17.6	24.6	58.2
10%	5m	0.0	6.0	15.0	21.0	0.0	28.5	71.4
	5m	0.0	2.5	0.5	3.0	0.0	83.3	16.6
	5m	0.0	2.0	0.0	2.0	0.0	100.0	0.0
	15m	0.0	3.5	0.0	3.5	0.0	100.0	0.0
	15m	0.0	1.0	0.0	1.0	0.0	100.0	0.0
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	23hrs	5.5	4.5	1.0	11.0	50.0	40.9	9.1
	24hrs	5.5	19.5	16.5	41.5	13.2	46.9	39.7
20%	5m	0.0	9.0	10.5	19.5	0.0	46.1	53.8
	5m	0.0	15.5	0.5	16.0	0.0	96.8	3.1
	5m	0.0	5.5	0.0	5.5	0.0	100.0	0.0
	15m	0.0	9.5	0.0	9.5	0.0	100.0	0.0
	15m	0.0	3.0	0.0	3.0	0.0	100.0	0.0
	15m	0.0	4.0	0.0	4.0	0.0	100.0	0.0
	23hrs	16.0	2.5	2.0	20.5	78.0	12.1	9.7
	24hrs	16.0	49.0	13.0	78.0	20.5	62.8	16.6
30%	5m	0.0	6.0	6.0	12.0	0.0	50.0	50.0
	5m	0.0	6.0	0.0	6.0	0.0	100.0	0.0
	5m	0.0	4.5	0.0	4.5	0.0	100.0	0.0
	15m	6.5	1.5	0.0	8.0	81.2	18.7	0.0
	15m	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	15m	3.0	0.5	0.0	3.5	85.7	14.2	0.0
	23hrs	16.0	13.5	1.0	30.5	52.4	44.2	3.2
	24hrs	25.5	32.0	7.0	64.5	39.5	49.6	10.8

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Table R

Water Intake (g) Before Food Deprivation (0%) and On Days When Birds Were Fed After a 10%, 20%, or 30% Body Weight Loss

BIRD NUMBERS	Percent Body Weight Loss			
	0%	10%	20%	30%
377	137.0	81.0	127.0	92.0
366	132.0	170.0	58.0	60.0
508	233.0	193.0	250.0	131.0
510	215.0	250.0	250.0	128.0
527	72.0	82.0	82.0	86.0
534	107.0	100.0	92.0	23.0

Table S

Means and Standard Deviations for Body Weight (g) in 15 Day Periods Before Trigeminal Deafferentation

Group	Bird Numbers	Extent of Deafferentation[a]	Periods 1 MEAN	Periods 1 SD	Periods 2 MEAN	Periods 2 SD
CHPV	400	2BR	567.3	10.4	567.4	2.9
	399	1BR	617.4	7.5	632.3	6.2
CKPV	393	2BR	673.3	7.1	693.8	3.9
	306	2BR	571.7	2.7	582.0	5.5
	394	2BR	587.0	6.9	593.5	4.1
	392	IN	495.3	2.8	484.3	5.1
HKP	341	2BR	555.0	5.0	561.5	2.9
	377	SC	569.3	5.9	575.3	5.4
	507	A	629.5	14.9	629.9	7.4
	526	A	587.4	6.6	598.6	11.6
KP	395	2BR	569.4	3.2	560.3	3.4
	405	2BR	571.3	4.8	568.8	4.1
	413	1BR	575.3	4.9	577.0	2.3
	310	1BR	607.1	6.6	596.4	7.9
	398	1BR	554.5	6.9	554.4	5.9

[a]1BR=one branch, 2BR=two branch, IN=indeterminate (see text), SC=surgical control, A=anesthetized only.

Table T

Means and Standard Deviations for Body Weight (g) in 15 Day Periods After Trigeminal Deafferentation

Group	Bird Numbers	Extent of Deafferentation[b]	Periods 3 MEAN	Periods 3 SD	Periods 4 MEAN	Periods 4 SD
CHPV	400	2BR	543.4	7.3	547.7	4.5
	399	1BR	615.4	23.6	650.0	5.6
CKPV	393	2BR	658.7	12.5	672.4	5.0
	306	2BR	558.9	16.1	567.7	3.8
	394	2BR	539.0	15.5	563.6	6.9
	392	IN	451.9	15.0	457.6	4.9
HKP	341	2BR	537.4	11.5	550.3	7.3
	377	SC	568.4	14.3	584.6	12.9
	507	A	630.3	4.4	631.1	2.2
	526	A	595.1	3.8	601.4	5.6
KP	395[a]	2BR	532.9	3.8	--	--
	405	2BR	528.4	13.3	537.3	10.0
	413	1BR	546.9	18.8	582.4	8.6
	310	1BR	579.4	18.8	592.4	6.5
	398	1BR	555.1	14.2	567.7	2.1

[a]There are no data for period 4.
[b]1BR=one branch, 2BR=two branch, IN=indeterminate (see text), SC=surgical control, A=anesthetized only.

Table U

Mann-Whitney U Tests on Body Weight Data in 15 Day Periods Before and After Trigeminal Deafferentation

Group	Bird Numbers	Extent of Deafferentation[b]	Direction of Differences					
			1vs.2	2vs.3	3vs.4	1vs.3	2vs.4	1vs.4
CHPV	400	2BR	1=2	2>3**	3=4	1>3**	2>4**	1>4**
	399	1BR	-	-	3<4**	-	2<4**	1<4**
CKPV	393	2BR	1<2**	2>3**	3<4*	1=3	2>4**	1=4
	306	2BR	1<2**	2>3**	3=4	1=3	2>4*	1=4
	394	2BR	1=2	2>3**	3<4**	1>3**	2>4**	1>4**
	392	IN	1>2**	2>3**	3=4	1>3**	2>4**	1>4**
HKP	341	2BR	1<2**	2>3**	3<4*	1>3**	2>4**	1=4
	377	SC	-	-	-	-	-	1<4*
	507	A	-	-	-	-	-	-
	526	A	1<2*	2=3	-	1<3**	-	1<4**
KP	395[a]	2BR	1>2**	2>3**		1>3**		
	405	2BR	1=2	2>3**	3=4	1>3**	2>4*	1>4**
	413	1BR	1=2	2>3**	3<4**	1>3**	2<4*	1=4
	310	1BR	1>2*	2=3	-	1>3**	2=4	1>4**
	398	1BR	-	-	3<4*	-	2<4**	1<4**

Note. Prior analyses of variance computed on the body weight data (1:2:3:4; 1:2:3; and 2:3:4) were significant ($p < .02$, or better except 1:2:3:4 for bird 377, $p < .05$) unless indicated (-).

[a] There are no data for period 4.

[b] 1BR=one branch, 2BR=two branch, IN=indeterminate (see text), SC=surgical control, A=anesthetized only.

*$p < .05$

**$p < .01$

Table V

Daily Seed Ingestion(g) of Bird 341 Pre and Postoperatively

	PRE			POST		
Days	Hemp	Kafir	Total	Hemp	Kafir	Total
1	8.0	25.5	33.5	21.5	16.0	37.5
2	5.0	21.0	26.0	10.0	21.0	31.0
3	10.0	13.0	28.0	22.0	0.0	22.0
4	4.0	24.0	28.0	22.0	13.0	35.0
5	14.0	19.0	33.0	6.0	19.0	25.0
6	8.0	20.5	28.5	25.0	1.0	26.0
7	16.0	14.0	30.0	22.0	8.0	30.0
8	10.0	21.0	31.0	6.5	16.5	23.0
9	19.5	5.0	24.5	21.0	0.5	21.5
10	9.0	19.0	28.0	18.0	10.0	28.0
11	10.0	17.0	27.0	7.5	4.0	11.5
12	16.0	8.0	24.0	20.0	1.0	21.0
13	13.0	19.0	32.0	18.0	10.0	28.0
14	9.0	20.0	29.0	7.5	10.0	17.5
15	16.0	7.0	23.0	16.0	14.0	30.0
16	14.0	24.0	38.0	21.5	9.0	30.5
17	7.0	21.0	28.0	21.0	11.5	32.5
18	16.0	6.0	22.0	20.0	12.5	32.5
19	12.0	21.0	33.0	18.0	11.5	29.5
20	7.0	21.0	28.0	15.0	11.5	26.5
21	20.0	4.0	24.0	11.5	11.0	22.5
22	19.0	23.5	42.5	18.0	11.0	29.0
23	10.0	19.5	29.5	20.0	8.5	28.5
24	17.0	8.0	25.0	18.5	14.0	32.5
25	13.0	26.0	39.0	15.0	10.0	25.0
26	9.0	19.0	28.0	17.0	14.5	31.5
27	15.0	14.0	29.0			
28	9.0	20.5	29.5			
29	5.5	20.0	25.5			
30	15.0	6.0	21.0			

Table W

Daily Seed Ingestion(g) of Bird 377 Pre and Postoperatively

Days	PRE				POST			
	Hemp	Peas	Kafir	Total	Hemp	Peas	Kafir	Total
1	10.0	0.0	16.0	26.0	14.0	1.0	15.0	30.0
2	5.0	3.5	18.0	26.5	3.5	18.5	3.0	25.0
3	11.0	9.0	4.0	24.0	24.0	17.0	0.0	41.0
4	3.5	6.0	19.5	29.0	16.0	0.0	19.5	35.5
5	4.0	6.0	14.0	24.0	5.0	18.0	13.0	36.0
6	12.5	13.0	4.0	29.5	20.0	12.0	0.0	32.0
7	3.0	6.0	22.0	31.0	11.0	1.0	15.0	27.0
8	4.0	11.0	14.0	29.0	1.0	20.0	6.0	27.0
9	8.0	17.0	3.0	28.0	22.0	22.0	0.0	44.0
10	5.0	4.0	20.0	29.0	13.5	0.0	17.0	30.5
11	6.0	8.0	16.0	30.0	2.5	20.0	8.0	30.5
12	7.0	10.0	10.0	27.0	15.0	14.5	0.0	29.5
13	7.0	5.0	18.0	30.0	14.0	1.5	10.5	26.0
14	5.0	8.0	15.0	28.0	2.0	24.0	3.5	29.5
15	3.5	9.5	8.0	21.0	11.0	18.5	0.0	29.5
16	8.0	4.0	19.0	31.0	6.0	11.0	10.5	27.5
17	3.0	8.0	15.0	26.0	4.0	14.0	1.0	19.0
18	13.0	17.0	3.0	33.0	9.0	24.0	0.0	33.0
19	4.0	5.0	21.0	30.0	2.0	23.5	10.0	35.5
20	6.0	14.0	11.0	31.0	7.0	23.0	5.0	35.0
21	15.0	14.0	2.0	31.0	8.5	23.0	0.0	31.5
22	8.0	5.0	20.0	33.0	0.0	21.0	12.5	33.5
23	5.0	10.0	14.0	29.0	10.0	24.0	0.0	34.0
24	8.0	16.0	2.0	26.0	11.0	22.0	0.0	33.0
25	8.0	5.0	17.0	30.0	1.0	24.0	9.5	34.5
26	11.0	13.0	14.0	38.0	9.0	25.0	0.0	34.0
27	8.0	19.0	2.0	29.0	7.0	23.0	0.0	30.0
28	7.0	7.0	19.0	33.0	1.0	20.0	14.0	35.0
29	4.5	11.0	11.0	26.5	8.0	20.0	5.0	33.0
30	12.0	19.0	3.0	34.0	4.5	22.0	6.5	33.0

Table X

Daily Seed Ingestion(g) of Bird 392 Pre and Postoperatively

	PRE			POST		
Days	Kafir	Vetch	Total	Kafir	Vetch	Total
1	12.0	17.5	29.5	3.0	18.0	21.0
2	12.0	15.0	27.0	0.0	18.0	18.0
3	11.5	17.0	28.5	15.0	11.0	26.0
4	11.0	20.5	31.5	16.0	9.0	25.0
5	11.0	16.0	27.0	7.0	17.0	24.0
6	13.0	15.5	28.5	10.0	14.0	24.0
7	15.0	15.0	30.0	15.5	10.0	25.5
8	12.0	16.5	28.5	14.0	11.0	25.0
9	12.5	15.0	27.5	5.0	17.5	22.5
10	11.0	15.0	26.0	12.5	13.0	25.5
11	9.0	11.5	20.5	13.5	7.5	21.0
12	21.5	12.5	34.0	14.0	8.0	22.0
13	8.0	12.0	20.0	10.5	8.5	19.0
14	14.5	11.5	26.0	12.0	9.0	21.0
15	14.0	10.0	24.0	12.5	6.0	18.5
16	9.0	13.0	22.0	11.0	10.0	21.0
17	10.5	11.5	22.0	4.0	9.0	13.0
18	12.5	14.0	26.5	12.0	5.0	17.0
19	7.5	10.5	18.0	12.0	4.5	16.5
20	8.0	13.0	21.0	11.0	7.0	18.0
21	10.0	11.0	21.0	7.0	7.5	14.5
22	10.0	8.0	18.0	8.0	10.0	18.0
23	11.0	9.0	20.0	11.0	7.5	18.5
24	9.5	7.5	17.0	8.0	5.0	13.0
25	11.5	6.0	17.5	8.0	8.0	16.0
26	10.5	6.5	17.0	9.0	10.0	19.0
27	6.0	10.0	16.0	11.0	4.0	15.0
28	8.0	6.5	14.5	10.5	6.0	16.5
29	12.5	4.0	16.5	7.0	10.0	17.0
30	10.5	5.5	16.0	13.0	1.0	14.0

Table Y

Daily Seed Ingestion(g) of Bird 399 Pre and Postoperatively

	PRE				POST			
Days	Hemp	Corn	Vetch	Total	Hemp	Corn	Vetch	Total
1	23.0	0.5	0.5	24.0	12.0	7.5	0.0	19.5
2	16.5	4.0	0.0	20.5	19.0	5.0	3.0	27.5
3	16.5	5.0	2.5	24.0	18.0	11.0	6.0	36.0
4	20.5	4.0	1.0	25.5	23.0	12.0	2.0	37.0
5	23.0	3.0	0.0	26.0	22.0	8.5	2.0	32.5
6	16.0	9.0	5.0	30.0	19.0	11.5	9.0	39.5
7	17.0	10.5	2.0	29.5	19.0	11.0	4.0	34.0
8	17.0	10.0	0.5	27.5	22.0	12.0	2.5	36.5
9	23.5	11.0	0.5	35.0	22.0	5.5	3.0	30.5
10	13.5	12.0	3.0	28.5	18.5	7.0	6.5	32.0
11	17.0	9.5	1.5	28.0	16.0	8.5	9.0	33.5
12	20.0	9.0	0.0	29.0	23.0	9.5	0.0	32.5
13	21.0	7.0	0.0	28.0	22.5	6.5	1.0	30.0
14	17.5	9.0	4.0	30.5	16.0	7.0	7.0	30.0
15	18.0	12.0	1.0	31.0	16.0	11.0	6.0	33.0
16	20.0	10.5	0.0	30.5	17.0	10.5	1.5	29.0
17	22.0	7.0	1.0	30.0	19.0	7.0	0.5	26.5
18	19.0	9.0	6.5	34.5	16.0	7.0	4.0	27.0
19	19.5	14.0	8.0	43.0	18.0	8.0	3.0	29.0
20	20.5	10.0	3.0	33.5	22.0	12.0	0.5	34.5
21	22.0	10.0	3.0	35.0	24.0	5.5	0.5	30.5
22	20.0	11.0	1.0	32.0	20.5	8.5	3.0	32.0
23	20.5	14.5	0.5	35.5	20.0	14.0	0.5	34.5
24	22.0	9.0	1.0	32.0	21.0	11.0	0.0	32.0
25	25.5	8.0	0.0	33.5	20.0	12.0	0.0	32.0
26	17.5	9.5	10.5	37.5	17.0	15.0	1.0	33.0
27	19.5	10.5	2.0	32.0	21.0	14.0	0.5	35.5
28	20.0	11.0	0.5	31.5	22.0	5.0	0.0	27.0
29	25.0	10.0	0.0	35.0	17.5	6.0	4.0	27.5
30	20.0	10.5	4.0	34.5	16.5	13.5	5.0	35.0

Table Z

Means and Standard Deviations for Total Daily Water Intake (g) in 15 Day Periods Before Trigeminal Deafferentation

Group	Bird Numbers	Extent of Deafferentation[a]	Periods 1 MEAN	Periods 1 SD	Periods 2 MEAN	Periods 2 SD
CHPV	400	2BR	148.3	22.1	144.0	20.0
	399	1BR	137.9	30.8	131.4	19.2
CKPV	393	2BR	36.1	5.3	33.3	2.4
	306	2BR	64.7	9.2	80.1	6.4
	394	2BR	57.5	8.3	63.9	10.6
	392	IN	46.9	10.7	32.3	9.2
HKP	341	2BR	47.3	11.1	47.4	18.0
	377	SC	67.9	7.7	64.9	8.3
	507	A	75.1	19.6	78.1	7.8
	526	A	132.9	18.4	164.1	18.6
KP	395	2BR	44.9	4.3	34.3	6.3
	405	2BR	46.9	4.3	56.0	6.7
	413	1BR	128.4	26.7	98.5	19.3
	310	1BR	116.6	10.3	172.5	27.5
	398	1BR	49.9	9.6	57.8	7.4

[a] 1BR=one branch, 2BR=two branch, IN=indeterminate (see text), SC=surgical control, A=anesthetized only.

Table AA

Means and Standard Deviation for Total Daily Water Intake (g) in 15 Day Periods After Trigeminal Deafferentation

Group	Bird Numbers	Extent of Deafferentation[b]	Period 3 MEAN	Period 3 SD	Period 4 MEAN	Period 4 SD
CHPV	400	2BR	73.6	15.9	100.0	11.8
	399	1BR	98.1	26.4	157.5	44.4
CKPV	393	2BR	46.9	5.2	46.0	5.1
	306	2BR	69.3	14.0	77.5	14.1
	394	2BR	59.0	5.0	65.4	7.7
	392	IN	34.2	4.9	26.8	4.5
HKP	341	2BR	39.5	10.9	56.2	7.5
	377	SC	62.5	11.9	74.1	17.2
	507	A	77.2	8.2	69.1	12.1
	526	A	163.9	19.1	169.0	43.3
KP	395[a]	2BR	33.5	8.2	--	--
	405	2BR	42.3	5.4	40.3	8.1
	413	1BR	54.8	6.4	111.1	29.0
	310	1BR	128.6	15.3	124.9	36.0
	398	1BR	59.1	8.4	51.8	7.2

[a]There are no data for period 4.
[b]1BR=one branch, 2BR=two branch, IN=indeterminate (see text), SC=surgical control, A=anesthetized only.

Table BB

Mann-Whitney U Tests on Water Intake in 15-Day Periods Before and After Trigeminal Deafferentation

Group	Bird Numbers	Extent of Deafferentation[b]	Direction of Differences					
			1vs.2	2vs.3	3vs.4	1vs.3	2vs.4	1vs.4
CHPV	400	2BR	1=2	2>3***	3<4***	1>3***	2>4	1>4***
	399	1BR	1=2	2>3**	3<4**	1>3**	2=4***	1=4
CKPV	393	2BR	1=2	2<3***	3=4	1<3***	2<4***	1<4***
	306	2BR	1<2***	2>3**	3=4	1=3	2=4	1=4
	394	2BR	-	-	3<4***	-	2=4	1<4**
	392	IN	1<2**	2=3	3>4**	1>3*	2=4	1>4***
HKP	341	2BR	-	-	3<4**	-	2<4**	1<4**
	377	SC	-	-	3<4*	-	2<4*	1=4
	507	A	-	-	3=4	-	2>4*	1=4
	526	A	1<2**	2=3	-	1<3***	-	1=4
KP	395[a]	2BR	1>2***	2=3		1>3***		
	405	2BR	1<2**	2>3***	3=4	1>3**	2>4***	1=4
	413	1BR	1>2*	2>3***	3<4***	1>3***	2=4	1=4
	310	1BR	1<2***	2>3**	3=4	1<3*	2>4***	1=4
	398	1BR	1<2*	2=3	3>4*	1<3**	2>4**	1<4**

Note. Prior analyses of variance computed on the daily water intake (1:2:3; 2:3:4 and 1:2:3:4) were significant (p< .05, or better) unless indicated (-).

[a]There are no data for period 4.

[b]1BR=one branch, 2BR=two branch, IN=indeterminate (see text), SC=surgical control, A=anesthetized only.

*p < .05
**p < .01
***p < .001

Table CC

Means and Standard Deviations for Total Daily Food Intake (g) in 15 Day Periods Before and After Nucleus Basalis Lesions

Bird Numbers	Rating Assigned to NB Damage		PRE				POST			
			Period 1		Period 2		Period 3		Period 4	
	LH	RH	Mean	SD	Mean	SD	Mean	SD	Mean	SD
316	2	2	29.2	5.1	29.7	5.0	24.6	5.6	25.4	4.5
376	2-3	1	30.2	3.9	29.9	3.2	27.9	5.8	31.3	2.8
382	1	1-2	23.9	3.8	25.4	5.0	23.9	3.8	22.7	2.6
329	0-1	2	32.8	4.9	34.4	5.7	31.7	7.2	37.5	3.6
9	0	1	25.5	3.5	25.4	2.8	24.0	4.5	23.3	3.3
335	0	0	26.5	4.0	25.3	4.7	23.0	5.0	19.6	4.5
370	0	0	27.9	4.8	32.6	3.9	30.4	7.4	28.5	4.8

Note. LH = left hemisphere, RH = right hemisphere, 0 indicates no damage, 1 = small, 2 = moderate, and 3 = complete damage. Subjects 335 and 370 were control animals which sustained damage to areas medial or dorsal to nucleus basalis (NB).

Table DD

Means and Standard Deviations for Total Daily Water Intake (g) in 15 Day Periods Before and After Nucleus Basalis Lesions

Bird Numbers	Rating Assigned to NB Damage		PRE				POST			
			Period 1		Period 2		Period 3		Period 4	
	LH	RH	Mean	SD	Mean	SD	Mean	SD	Mean	SD
316	2	2	129.1	33.3	136.9	28.0	180.6	63.9	235.2	22.4
376	2-3	1	98.6	50.8	69.6	9.4	41.8	9.3	54.9	13.9
382	1	1-2	71.3	16.8	69.9	13.0	79.8	18.3	91.2	21.6
329	0-1	2	61.8	9.9	69.7	36.2	46.9	11.1	61.6	13.0
9	0	1	160.4	31.6	129.6	28.2	100.2	33.4	92.0	27.2
335	0	0	130.8	25.8	93.0	14.8	65.6	16.6	70.9	13.8
370	0	0	45.4	9.4	47.4	7.1	33.5	9.5	40.6	11.2

Note. LH = left hemisphere, RH = right hemisphere, 0 indicates no damage, 1 = small, 2 = moderate, and 3 = complete damage. Subjects 335 and 370 were control animals which sustained damage to areas medial or dorsal to nucleus basalis (NB).

Table EE

Mann-Whitney U Tests on Water Intake in 15 Day Periods
Before and After Nucleus Basalis Lesions

Bird Numbers	Rating Assigned to NB Damage: LH	RH	Direction of Differences: 1vs.2	2vs.3	3vs.4	1vs.4	2vs.4	1vs.3
316	2	2	-	-	3<4***	1<4***	2<4***	-
376	2-3	1	1>2**	2>3***	3<4**	1>4***	2>4*	1<3***
382	1	1-2	-	-	3=4	1<4***	2<4**	-
329	0-1	2	1<2*	2>3**	3<4***	1=4	2=4	1<3***
9	0	1	1>2**	2>3*	3=4	1>4***	2>4**	1>3***
335	0	0	1>2**	2>3***	3=4	1>4***	2>4**	1>3***
370	0	0	1<2*	2>3**	3<4*	1>4*	2=4	1>3***

Note. LH = left hemisphere; RH = right hemisphere; 0 indicates no damage; 1 = small; 2 = moderate; and 3 = complete damage. Birds 335 and 370 were control animals which sustained damage to areas medial or dorsal to nucleus basalis. Differences indicated refer to preoperative periods 1 and 2 and postoperative periods 3 and 4. Prior analyses of variance computed on the daily water intake were significant ($p < .02$ or better except 2:3:4, bird 382 where $p < .05$) unless indicated (-).

* $p < .05$

** $p < .01$

*** $p < .001$

LIST OF ABBREVIATIONS

E - ectostriatum

FA - fronto-archistriate tract

HA - hyperstriatum accessorium

HD - hyperstriatum dorsale

His - hyperstriatum intercalatus superior

HV - hyperstriatum ventrale

HvDv - hyperstriatum ventrale dorsoventrale

HVvv - hyperstriatum ventrale ventroventrale

LH - lamina hyperstriatica

LPO - lobus parolfactorius

MD - medullaris dorsalis

N - neostriatum

NB - nucleus basalis

PA - paleostriatum augmentatum

QFT - quinto-frontal tract

TO - tuberculum olfactorium

TTD - spinal trigeminal nucleus

Va - vallecula

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