The Condor 97:1041–1047

MOTILITY RESPONSES TO FASTING IN THE GASTROINTESTINAL TRACT OF THREE AVIAN SPECIES[1]

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Abstract. To better understand responses of the avian gastrointestinal tract to fasting, fifteen domestic fowls (*Gallus*), two Ring-necked Pheasants (*Phasianus*), and two Barred Owls (*Strix*) were implanted with chronic Ag-AgCl electrodes and extended myoelectric recordings were made during different degrees of feeding or fasting. The motility responses are described, especially single, strong, spike potential bursts (SPBs) that rapidly propagated in an orad direction. The best explanation for our observations seems to be that when the food in the lumen of the upper digestive tract of a chicken begins to be exhausted, fed-state activity in the gizzard and duodenum is restimulated for a short period by single orad SPBs that propagate rapidly from the distal ileum. This stimulation presumably results from nutritive material being moved into the duodenum and gizzard. When one SPB becomes insufficient to stimulate upper-tract activity, orad SPBs begin to occur more frequently. Eventually the stronger rhythmic oscillating complex (ROC) occurs when SPBs no longer elicit fed-state activity. The ROC's extended activity presumably moves nutritive material more effectively than single SPBs. After a ROC, fed-state activity in the stomach and duodenum continues for a longer period (30–60 min in birds fasted for 24 hr). Both SPBs and ROCs continue to occur as long as a bird fasts (≥80 hr). Single strong orad SPBs and prolonged ROCs appear to be successive mechanisms whereby, in times of food deprivation, the gut maximizes its nutritive resources by recycling whatever food still remains within the digestive system. This system exists in the two galliforms studied, but apparently not in Barred Owls.

Key words: *Intestinal motility; fasting; domestic fowl;* Gallus gallus; *Ring-necked Pheasant* (Phasianus colchicus); *Barred Owl* (Strix varia); *digestion.*

INTRODUCTION

During a series of experiments in which we used myoelectric recordings to study the gastrointestinal motility of birds while they were in fed and fasted states (Clench et al. 1989), we noted the characteristic fed-state motility patterns that occurred when food was present in the digestive tract. Then, as the quantity of food diminished in the lumen, the fed patterns first slowed and finally ceased, and other types of motility began. In addition to the usual fed-state patterns (clusters of duodenal spike potentials coordinated with gastric activity and frequent, random, low-amplitude spike potentials in the ileum; Fig. 1), two other distinctive motility responses to fasting were recorded; they both restimulated fed-state myoelectric activity. The first we named the rhythmic oscillating complex (ROC). The ROC is a highly organized pattern of rapidly propagating bursts of spike potentials that alternate direction in a regular and predictable manner, with a mean of 78.9 orad and aborad action potentials extending over 7.6 min in *Gallus* (Clench and Mathias 1992a, 1992b). The second and most common type of event recorded during fasting is discussed here: single, strong, spike potential bursts (SPBs) that rapidly propagated in an orad direction—the myoelectric representation of single retrograde ring contractions.

METHODS

Fifteen of the study subjects were young, but fully grown, large male domestic fowls (*Gallus gallus*) of three different breeds: nine Barred Rock, four wild-type "gamecocks," and two Heiseldorf-Nelsons. Four other birds, two Ring-necked Pheasants (*Phasianus colchicus*) and two Barred Owls (*Strix varia*), were also studied.

Under anesthesia induced by intramuscular injections of pentobarbital sodium (25 $mg^{-1} \cdot kg^{-1}$) or ketamine hydrochloride and xylazine hydrochloride (25 and 1.5 $mg^{-1} \cdot kg^{-1}$, respectively), subjects were chronically implanted with miniature bipolar silver-silver chloride electrodes (silver tips 1.0 mm apart) constructed in our labo-

[1] Received 27 March 1995. Accepted 26 June 1995.

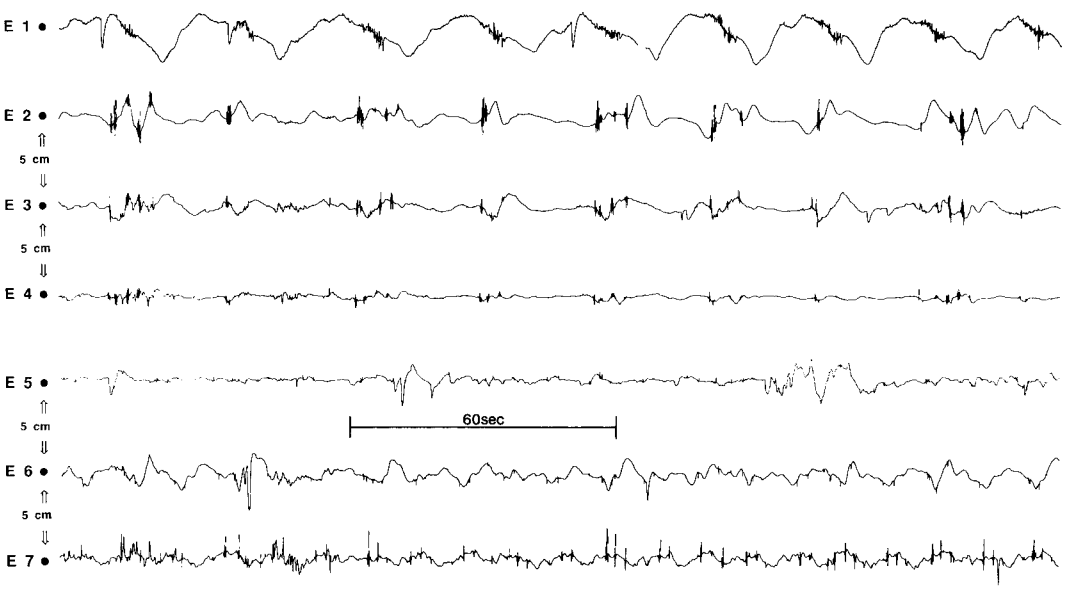

FIGURE 1. Fed-state myoelectric activity in a male chicken. Electrode 1 is on the thick muscle of the stomach; E2–E4 are 5 cm apart on the duodenum, with E3 at the duodenal flexure; E5–E7 are 5 cm apart on the proximal ileum. Note the slow-wave activity, particularly in the stomach, the clusters of duodenal spiking coordinated with gastric activity, and the random spiking of the ileum. Reproduced with permission from The American Physiological Society (Clench and Mathias 1992a).

ratory (Clench et al. 1989). The seven smaller roosters were implanted with four electrodes and the eight largest were given seven. The electrodes were sutured to the intestinal serosa in several different locations: two to seven electrodes were placed 2.5, 5, or 10 cm apart on the ileum of all chickens. (Because there is no morphological basis in birds for differentiating the small intestine distal to the duodenum as "jejunum" and "ileum," we use the term "ileum" for that entire length of intestine.) The spacing and placement of the electrodes was determined by the length of each bird's ileum and the particular motility characteristic being studied. In three of the roosters, one electrode was implanted on the thick cranioventral muscle of the stomach and three more were placed 4 or 5 cm apart on the duodenum. In related studies, some of the four electrodes were sutured on the ceca and the rest on the ileum; the ileal record of those birds is reported here. The pheasants were implanted with four electrodes spaced 5 cm apart on the proximal ileum and the owls received four electrodes 2.5 cm apart in the same area.

Silver wires that lead from the electrodes had been soldered previously to a 7- or 15-pin connector (ITT Cannon Electric) and a curved saddle of dental acrylic constructed around its base to fit the contour of a bird's neck. During surgery, the electrodes and the wires leading from them to the connector were tunneled under the skin from an incision on the back of the neck through a ventral midline incision and into the abdominal cavity. After the electrodes were sutured to the intestinal tract, both incisions were closed and the top of the connector was left exposed on the back of the neck. This allowed the birds to be connected by a flexible braided lead to an 8-channel R612 physiological recorder fitted with model 9806 couplers (SensorMedics). A week or more after surgery, recording sessions began with the birds comfortably unrestrained in a large cage covered loosely with a dark cloth. Because all three species under study had crops and thus the quantity of food present in the upper digestive tract could not be predicted after a given time period when food was not available, birds were determined to be in the fed or fasted state by their recorded motility patterns. Water was available to the birds while they were being recorded, but food was not. The recording sessions for the three species lasted for means of 5.9 to 6.2 hr each, and were made during normal daylight hours about twice a week until the silver tips of the electrodes became too corroded to produce a readable signal. Body mass of the sub-

jects was monitored throughout the study, and the feeding/fasting schedule adjusted so that each bird returned to its base weight (or higher) before being fasted again. All birds maintained or gained mass throughout the period of investigation.

The study was conducted under protocol approved by the Animal Care and Use Committee of The University of Texas Medical Branch at Galveston and under similar approval at the University of Virginia, Charlottesville, and the Veterans Administration Medical Center, Gainesville, FL. The domestically raised roosters and pheasants were housed in approved animal care facilities and maintained on standard commercial poultry diets: Layena crumble in Florida and Virginia, whole scratch grains in Texas (both products, Purina Mills). The owls were wing-crippled birds borrowed from rehabilitation centers; they were fed on thawed chicks and mice. After the recordings were completed, most of the galliforms were euthanized by an intravenous overdose of pentobarbital sodium. We removed the connectors from a few of the roosters, but left the silver electrodes and wires in place to avoid disturbing the abdominal cavity a second time. The birds' condition was then monitored on a long-term basis to assess negative effects of the implants; none were noted. The owls were studied later than most of the chickens and were returned to their respective nature centers after they had been reanesthetized and their connectors removed. They are reportedly continuing to do well in captivity.

Data from the recordings were analyzed by the Student's t test, with $P < 0.05$ considered significant.

RESULTS

The roosters yielded a mean of 8.8 recordings per bird, in a total of 132 sessions: 310.6 hr when they were in the fed condition and 466.8 hr while fasting. The pheasants were recorded a total of 12 times: 62.9 hr fed and 80.5 hr fasted. The owls were recorded a total of 16 times: 48.7 hr fed and 50.1 hr fasted.

SINGLE ORAD-PROPAGATING SPIKE POTENTIAL BURSTS (SPBs)

When a previously well-fed chicken was fasted and the upper digestive tract presumably had exhausted its crop-stored food, fed-state motility patterns slowed and then ceased and single strong orad-propagating SPBs appeared. These bursts were similar in rapid velocity and short duration (41.2 ± 2.3 cm/sec and 1.3 ± 0.0 sec, respectively; Clench and Mathias 1992a) to the orad spike component of a ROC; the SPBs all also apparently began in the distal ileum, traveled the full length of the small intestine, and usually extended into the stomach. They occurred one at a time, never in the clusters typical of duodenal spiking. The SPBs did not originate or occur in the ceca (unpublished observations). Because of the strong motility differences that are found between the small and large bowel (cf. Lai and Duke 1978, Duke 1989), we doubt that SPBs occur in the colon and migrate into the ileum. However, as we did not record the ileum and colon together, this point remains to be determined.

Day-long recordings made while the intestinal tract shifted from a fed to a fasted state showed that orad SPBs did not appear while gastric and duodenal activity remained at a high level. When that level diminished, however, strong retrograde spikes began to occur (Fig. 2). We counted the number of orad spikes per 30-min period, beginning 30 or 60 min after a recording began. In chickens, when gastroduodenal activity was high (a mean of 54.6 ± 6.6 duodenal spike clusters per 30 min), no SPBs spikes occurred. When that activity had dropped to a mean of 32.8 ± 14.1 clusters/30 min, a mean of one spike occurred during the period, and when gastroduodenal activity had slowed to a mean of 16.3 ± 4.1 clusters/30 min, a mean of two SPBs was recorded. Shortly thereafter, gastroduodenal activity ceased and a ROC began within 30 min.

When the gut began to run out of food but still apparently had some nutritive material in the lumen, an orad SPB invariably caused increased duodenal and gastric activity (Fig. 2). As time went on, this stimulated fed-state activity lasted for a shorter and shorter period, and multiple orad spikes became necessary for a reaction to take place.

In the well-fasted chicken gut (one for which no food had been available for 18 to 24 hr, and, thus, was unlikely to be present in the lumen), orad spikes occurred even more frequently. This spiking also seemed to stimulate gastroduodenal myoelectric activity, but to a lesser degree than when the intestine had recently been in the fed state. In the well-fasted gut, the mean number of duodenal clusters recorded per 30 min in the absence of orad spiking was 7.7 ± 0.8 ($n = 48$, 30-min periods); but duodenal activity increased significantly when orad spiking was recorded during the count period: 15.9 ± 2.5 ($n = 20$) with

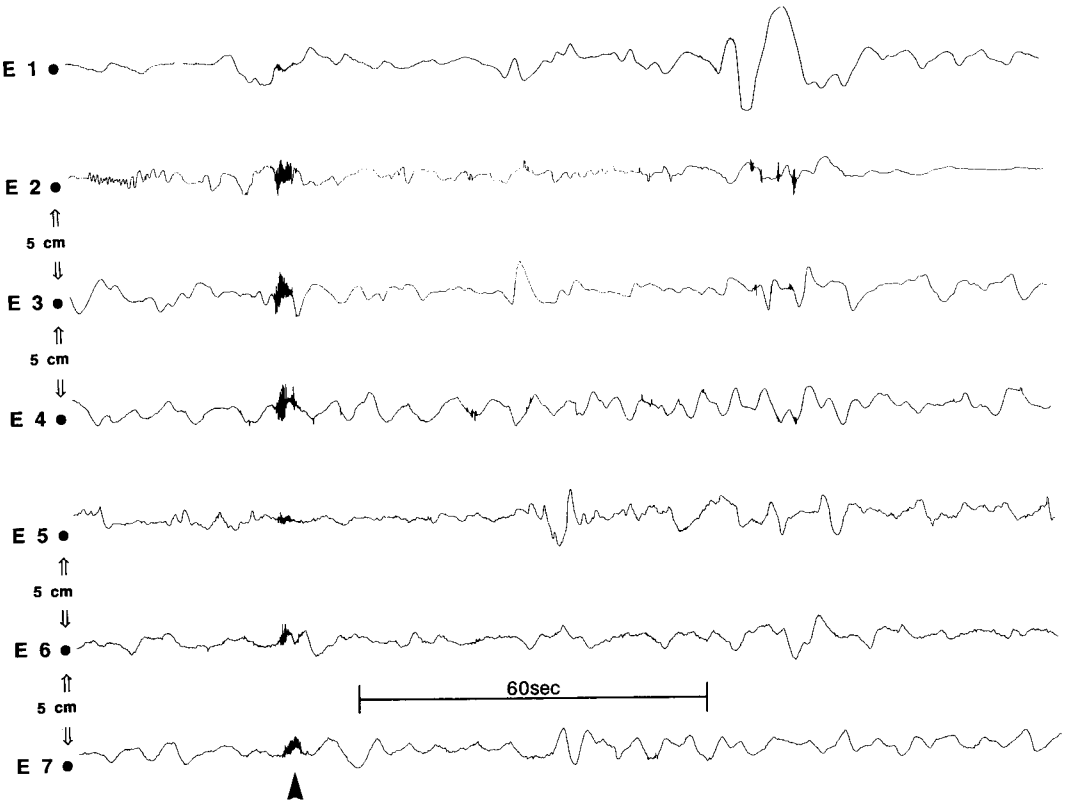

FIGURE 2. Single strong orad SPB (arrow) in a well-fasted male chicken; conventions as in Figure 1. Note that the SPB is on the slow wave and propagates rapidly from ileum to stomach; a cluster of duodenal activity (E2–E4) occurred after the SPB.

one SPB and 18.0 ± 2.5 (n = 20) with two or more (both $P < 0.0001$).

Because the pheasants had electrodes only on the ileum, we could not analyze the relative occurrence of the SPBs in relation to gastric and duodenal activity. Pheasants, however, did exhibit the same type of SPBs as chickens, but the propagation velocity was slower (3.05 ± 0.15 cm/sec) and the duration was longer (5.9 ± 0.3 sec). Despite long recording periods while both fed and fasted, the owls showed no evidence of SPBs. Nor did the owls demonstrate ROCs (Clench and Mathias 1992a), possibly for the same unknown reason.

RELATIONSHIP BETWEEN SINGLE ORAD-PROPAGATING SPIKE POTENTIAL BURSTS AND MIGRATING MYOELECTRIC COMPLEXES

On several occasions we recorded in both chickens and pheasants single strong orad spikes as they moved through the regular spike activity phase (phase III) of migrating myoelectric complexes (MMCs) (Fig. 3). The only disruption caused by the SPB was that after it passed through, the next slow wave lacked regular MMC-type spike activity; all the slow waves thereafter contained the typical MMC spike activity (if slightly diminished in amplitude) and the complex ended normally. Figure 3 shows an orad spike passing through an MMC in a pheasant. Roche (1974, Fig. 4E) also illustrated the brief inhibition caused by an orad spike passing through what he termed "localized or slow propagated hyperactivity" (which we interpret as an MMC) in the chicken.

DISCUSSION

Duke and colleagues (Duke et al. 1972, Duke and Evanson 1972, Dziuk and Duke 1972, Savory et al. 1981, Duke et al. 1989) found that reflux of duodenal contents into the stomach was both common and frequent and that refluxes of distal small intestine and duodenum were strong-

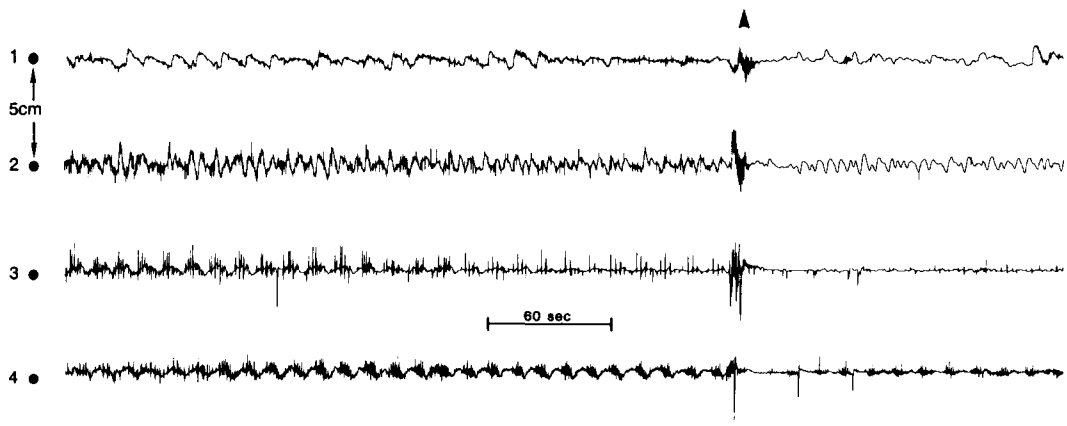

FIGURE 3. Male pheasant implanted with four ileal electrodes, 5 cm apart. A single orad SPB (arrow) passed through a migrating myoelectric complex (MMC) that was occurring on electrodes 3 and 4, only briefly disturbing the MMC activity.

ly synchronized; turkey intestinal refluxes were double (two-peaked) contractions, those of chickens were single. Their studies in turkeys confirmed and greatly amplified the early reports from chickens (Vonk et al. 1946) and were in turn confirmed by the studies of others (Oguro and Ikeda 1974). Duke and colleagues properly termed it "reflux" because their data were recorded from strain gauges and electrodes and were correlated with radiographic observations and recordings of intraluminal pressure changes; the luminal contents were, indeed, refluxing. Duke and colleagues did not, however, correlate the frequency of reflux with the quantity of food being processed by the system, apparently because they lacked data from the fasted state; their birds had food available during recording. Based on the results of the present study, we suggest that the birds' fed condition determined the frequency of reflux reported by Duke and colleagues—about every 15–20 min or ~4 times/hr in turkeys (Duke et al. 1972) and ~5–6/hr and ~10–12/hr in the distal small intestine and duodenum, respectively, of Leach's Storm-petrel (*Oceanodroma leucorhoa*; Duke et al. 1989).

The present study also shows that the term "duodenal" reflux may be a misnomer; this activity begins at least as distal as the distal ileum. Duke et al. (1975a) found that the duodenal reflux in turkeys also involved the distal small intestine, but only 26.7% of the time. What we term single, strong orad SPBs is probably the same phenomenon, yet we found that it *always* originates distal to the duodenum. The problem here may just be one of terminology, but it is also possible that chickens and turkeys differ in this aspect of their physiology. It is also puzzling, however, that in the figures used by Duke and colleagues to illustrate reflux, the action potentials show duodenal activity beginning *before* that in the ileum (Duke et al. 1975a, Fig. 3) or that the distal duodenal activity is not convincingly earlier than that in the proximal duodenum (Duke et al. 1975b, Fig. 6). Because of these inconsistencies, and because we have not yet studied birds myoelectrically and radiographically at the same time, we are avoiding "reflux" in our terminology.

The best explanation for the patterns observed in the myoelectric recordings from our studies seems to be the following: when the food supply in the upper digestive tract of a fasted chicken begins to be exhausted, fed-state activity in the gizzard and duodenum can be restimulated for a short period by single orad SPBs that propagate rapidly from the distal ileum; this stimulation presumably results from nutritive material being moved back up into the duodenum and gizzard by the orad contractions. Over the next few hours, single SPBs become insufficient to stimulate upper-tract activity, and SPBs begin to occur more frequently (usually two or three, but occasionally as many as ten in a 30-min period). The spikes always stop as soon as the duodenum shows fed-state activity. Eventually an extended complex, the ROC, occurs when single orad spikes no longer elict fed-state activity in the upper part of the tract; presumably too little nutritive material re-

mains in the lower tract to be moved by even a series of single contractions. The extended activity of a ROC appears to move nutritive material more effectively than can single contractions. After a ROC, fed-state activity in the stomach and duodenum continues for a longer period (lasting between 30–60 min in roosters fasted for 24 hr; Clench and Mathias 1992a), suggesting that a larger amount of nutritive material had been moved into the upper tract and is stimulating digestive activity. Both the single SPBs and ROCs continue to occur as long as a bird fasts, even for as long as 80 hr (the longest period we deprived a study subject of food; Clench and Mathias 1992a).

In summary, single strong orad SPBs and ROCs appear to be successive mechanisms whereby the gut maximizes its nutritive resources in times of food deprivation by recycling whatever is still available within the digestive system. That SPBs and ROCs are probably simple and complex versions of the same process is suggested by their similar physiological effects (stimulating the fed state) and the fact that they occur together in some species (galliforms) but are both lacking in others (owls).

Digestion theory has predicted that to maximize the rate of obtaining energy when the rate of ingestion is limited, an animal should prolong digesta retention (Sibly 1981). One case of retention has already been shown to occur in birds, but perhaps just in the proximal gastrointestinal tract. Duke et al. (1980) reported that captive Barred Owls increased both digestion time and thoroughness when fed at a sub-maintenance level: in hungry owls, the period between ingestion of a mouse and the following regurgitation of a pellet was prolonged, and the pellet contained a significantly smaller proportion of the meal than when the owls were on a maintenance diet. The data we have presented here and previously (Clench and Mathias 1992a) now add to this aspect of digestion theory by demonstrating a potential mechanism for recycling food in the central part of the digestive tract.

Where the recycled nutritive material may originate is still unknown, but the ceca have been suggested (Clench and Mathias 1992a). This SPBs/ROCs system exists in the two galliform species studied, which have large functional intestinal-type ceca (Clench and Mathias 1995). Single strong orad SPBs and ROCs do not seem to occur in Barred Owls, which have a secretory-type cecum of unknown function. Another potential source of nutritive material may be sloughed epithelial cells from the tips of the villi. Epithelial cells originate in the crypts (intestinal glands or glands of Lieberkühn) at the villous base and migrate rapidly to the villus tips. Depending on the villous length and location, this process can take from two to five days in young chickens; it accelerates over the longer villi in older birds with perhaps a 10-day replacement time in adults (Imondi and Bird 1966, Moon and Skartvedt 1975). When the cells reach the extrusion zone of the tip, they are routinely sloughed off into the lumen, and it may be these epithelial cells being stripped off the villi and moved orally by the single strong SPBs and ROCs that are stimulating a fed state.

ACKNOWLEDGMENTS

This study was partly supported by funds from the Medical Research Service of the Veterans Administration and the Departments of Internal Medicine at The University of Virginia and The University of Texas Medical Branch at Galveston. We thank Gary E. Duke and an anonymous reviewer for suggestions that improved the paper.

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