1. GASTROINTESTINAL PHYSIOLOGY

FOOD INGESTION

Ingested foodstuff contributes to an increase in the overall weight of an animal, but it does not become an integral part of the structure or metabolic activities of the animal, until it is absorbed somewhere through the digestive tract. What is not absorbed is discarded in the faeces as waste. The gastrointestinal tract provides a conduit through which all food has to pass. The first step in the use of such a conduit is to acquire, chew and swallow the food (Fig. 1-1).

Prehension

Animals achieve this basic step through the process of prehension. Depending on the species and age, animals use different modalities to ingest food. There are specific anatomical adaptations which permit an animal to ingest food in a given manner (Fig. 1-2).

Prehension by cattle

- Use the tongue to manipulate food into the mouth
- Use mobile lower teeth and hard palate to press and tear

Avian species use their beak or bill to pick up food. They do not masticate the food, but they do cover it with a mucus layer in order to facilitate swallowing (Fig. 1-7).

Mastication

Some species require significant mastication prior to swallowing, while others, such as most ruminants, masticate very little prior to swallowing. This strategy permits the collection of a significant volume of food in the rumen, and then, they start a process of rumination. Rumination consists of regurgitating portions of the ingested food to thoroughly masticate it, to reduce the particle size. This activity is normally conducted while the animal is resting in a recumbent position.

Carnivores do not significantly masticate their food; instead, they depend on a very aggressive enzymatic digestion to reduce particle size. They only masticate their food enough to reduce it to a swallowable size. Avian species do not have teeth to masticate (Fig. 1-8).
They depend on the production of mucus to coat the particles prior to swallowing, and then, they macerate the food within a specialized organ (the gizzard) that may contain a variety of hard materials, which the animal has purposely ingested. Commonly ingested pebbles help, through a grinding action, in the reduction of the particle size. Herbivores masticate their food not only to reduce the size of the particles but also to break the cellular wall of the food material, thus permitting the access of digestive enzymes. Smaller particles also reduce the incidence of damage to the walls of the gastrointestinal tract (GIT) (Fig. 1-9).

**Mastication in herbivores**

- **Reduce particle size**
  - Increases surface area
  - Breaks cellulose membrane
- **Lubricate for swallowing**
- **Mix with saliva**
- **Expose to digestive enzymes**
- **Reduce excoriation of GIT**

![Figure 1-9. Role of mastication in herbivores](image)

**Deglutition**

- **One voluntary initial stage**
  - Movement of bolus to back of oral cavity
- **A pharyngeal stage (involuntary)**
  - Passage from oral cavity to esophagus
- **Esophageal stage (involuntary)**
  - Passage of food into stomach

![Figure 1-10. Steps involved in deglutition](image)

**Deglutition**

Once the food has been masticated, it has to be swallowed. This process requires an initial voluntary stage which is to move the bolus towards the back of the oral cavity. Then, an involuntary reflex, which permits the passage of the bolus from the oral cavity to the esophagus without entering the trachea and the respiratory system, is activated (Fig. 1-10).

Most of the time, an animal maintains an open passage between the nose or mouth to the trachea, thus permitting the passage of air into the lungs and minimizing the entrance of air into the digestive system (Figs. 1-11, 1-12).

When there is food to be swallowed, a passage from the mouth to the oesophagus has to be created to permit
movement of the food. This passage is achieved by the elevation of the soft palate, which prevents the food from entering into the nasal cavity, and by the movement of the epiglottis backwards, which blocks the entrance to the trachea and opens the passage towards the oesophagus. All these changes, which take place in a very rapid sequence are involuntary and constitute the process of deglutition (Fig. 1-13) at which time the respiratory process is temporarily suspended.

**THE DIGESTIVE TRACT**

Most related species have similar anatomical components in the digestive tract, with slight differences in size, shape and sometimes regulation of the function of each component.

**Basic anatomy**

The gastrointestinal wall is made up of several layers. The outermost serosa is lined by a muscular layer which lies longitudinally to the tract and then the innermost layer of muscle consist of circular fibres. Towards the center is found the submucosa and the mucosal layers (Fig. 1-14).

Within the mucosa, there are a series of smooth muscle fibres, which form the muscularis mucosa. The muscle fibres are grouped in individual parallel bundles, connected to others by multiple gap junctions along its length. Each bundle is surrounded by connective tissue with a fusion point in between, forming a network of muscles functioning as a syncytium (Fig. 1-15).

**Physiology of the GIT**

The syncytium permits that an action potential, which is generated at some point, can move in all directions. Furthermore, there are connections between the longitudinal and circulatory layers which permit the
synchronization of movements to either mix or propel the intestinal content.

To control the tone and the motor activity of the gut, the membrane of the smooth muscle is continuously stimulated by intrinsic electrical activity in the form of slow waves or spikes. Variation in the changes of frequency of the membrane potential creates the rhythm of the slow waves (range from 3-12/min). What ultimately changes to create the slow waves is the membrane resting potential (Fig. 1-16).

**Electrical stimulation**

- **Continuos slow intrinsic activity**
  - Slow waves
  - Spikes
- **Slow waves (3 - 12/min) result by changes in resting membrane potential (range 5-15 mV) (from -50 to -35 mV)**
- **Controls spike potential that initiates contraction**

![Figure 1-16. Characteristic of the electrical activity in the intestinal tissue](image)

The counterparts of this process are the factors that trigger a spike. The resting membrane potential of the smooth muscle has to be larger than -40 mV. These spikes trigger a true action potential, which in turn controls contractile activity. The spike potential increases in frequency when the slow wave resting membrane potential is higher (Figs. 1-17, 1-18).

The more depolarized the membrane becomes, the more excitable it is and the more chances it has of contractile activity. The mechanism for achieving this higher membrane potential is presumed to be through an influx of Ca^{++} through calcium-sodium channels as opposed to the faster sodium channels used by nerve fibres.

Several factors contribute to the depolarization of the fibre's membranes. Physical distension (stretching) of the muscle, usually due to the presence of food in the tract; acetylcholine stimulation as well as parasympathetic stimulation by neurones secreting acetylcholine; and finally, several gastrointestinal hormones (Fig. 1-19).

The counterparts of this process are the factors that contribute to the hyper-polarization of the membranes. These are the effects of norepinephrine or epinephrine on the membranes and the sympathetic stimulation whose nerves secrete norepinephrine (Fig. 1-20).
Regulation of gut motility

Enteric nervous system. Regulation of all contractile and secretory activity is supported by an independent nervous system imbedded in the wall of the gut. This system is called the enteric nervous system and it extends the length of the GIT starting in the esophagus. The total number of neurons is as large as those found in the spinal cord. The enteric nervous system is made up of two plexuses: one located between the longitudinal and circulatory muscle layer called the Myenteric or Auerbach’s plexus and the other is found in the sub mucosal layer and is called the sub mucosal or Meissner’s plexus (Figs. 1-14, 1-21, 1-22). These two are interconnected in order to synchronize GIT functions.

Motility of the gut is primarily controlled by the myenteric plexus, while the secretory activity and blood flow are controlled mainly by the submucosal plexus.

Factors depolarizing membranes (membrane potential less negative)

- Stretching
- Acetylcholine
- Parasympathetic stimulation
  - Mediated through acetylcholine
- Specific gastrointestinal hormones

Factors hyperpolarizing membranes (membranes potential more negative)

- Norepinephrine or epinephrine on fibre membrane
- Sympathetic stimulation
  - Secreting norepinephrine

The enteric system is capable of controlling gastrointestinal functions independent of other body functions. However, on top of being connected between themselves, the two plexuses are further innervated by the sympathetic and parasympathetic systems. This innervation permits overall inhibition or stimulation of the gastrointestinal activities (Fig. 1-23).

Motility of the gut is primarily controlled by the myenteric plexus, while the secretory activity and blood flow are controlled mainly by the submucosal plexus.
There are multiple mechanisms through which the myenteric plexus controls motor activity throughout the gut (Fig. 1-24).

The myenteric plexus can increase the tonic contraction of the intestinal wall as well as the intensity and the rate with which the rhythmical contractions take place. Finally, stimulation of the myenteric system can result in faster conduction of excitatory waves along the intestinal wall and, as a result, there is an increase in peristaltic movement.

Although most of the activities of the myenteric system are excitatory in nature, there are also some inhibitory elements. These elements are believed to be mediated through the release of peptides; the most plausible candidates are those with vasoactive intestinal polypeptide (VIP). The action of these peptides appears to be focused in inhibiting sphincter activity (pyloric and ileocecal), thus modifying the rate of food passage into the duodenum and cecum respectively.

The submucosal plexus in turn controls secretory, absorptive and contractile activity in very small discrete sections of the GIT (Fig. 1-25).

**Submucosal plexus**

- **Controls the function of small sections of the intestine**
- **Signal from epithelium to SMP controls**
  - Local secretion
  - Local absorption
  - Local contraction
    - Regulate folding of gastrointestinal mucosa

The appropriate response is usually prepared and implemented by a signal that is generated by sensors in the epithelium of the gut which then is conveyed to the submucosal.

**Neurotransmitters.** A large number of neurotransmitters (Fig. 1-26) have been identified as participating in the regulation of gastrointestinal activity, but their specific roles are yet to be determined.
Gastrointestinal reflexes. The overall regulation of gastrointestinal function is based on reflexes controlled by the enteric, sympathetic and parasympathetic systems. These are reflexes which are integrated within the enteric system and are responsible for secretion as well as food mixing and peristalsis of the GIT (Fig. 1-27).

Other types of reflexes transmit information through long distances in the GIT. They require the participation of the gut as the starting point, integration in the sympathetic ganglia and response by another section of the gut. Among these we find the gastrocolic reflex which is responsible for the evacuation of the colon; the enterogastric reflex which involves the participation of the small intestine, and the colon which sends signals to reduce stomach motility and its secretion; and the colonoileal reflex which signals from the colon to reduce or prevent emptying of ileal contents into the colon.

There is still another type of reflex which involves the larger trajectory from the gut to the spinal cord and / or brain and back to the GIT. Through this type of reflex the duodenum, based on the rate at which it receives food, is capable of controlling gastric motor and secretory activity. In addition, reflexes that involve pain use these mechanisms to reduce overall gastrointestinal activity. Finally, faeces accumulation in the colon triggers the defecation reflex via signals sent to the spinal cord and back resulting in contraction of the colon, rectum and abdomen in order to defecate. As hinted earlier, many hormones influence different aspects of motility of the GIT and some influence both motility and secretion of the GIT (Fig. 1-28).

Cholecystokinin is a powerful compound secreted by I cells of the duodenum and jejunum which, in response to the presence of fat digestion by-products, fatty acids and monoglycerides, triggers contraction and emptying of the gallbladder. This makes bile salts available in the small intestine which emulsify the fats coming from the stomach. At the same time, cholecystokinin inhibits stomach motility, thus reducing the rate of stomach emptying into the duodenum and permitting better digestion. A similar effect is seen when fat and proteins are being emptied into the

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**Neurotransmitters**

- Acetylcholine
  - Mainly excites GI activity
- Norepinephrine
  - Usually inhibits GI activity
- Adenosine triphosphate (ATP)
- Serotonin
- Vasoactive intestinal polypeptide (VIP)
- Somatostatin (SS)
- Leu-enkephalin
- Met-enkephalin
- Bombensin

**Gastrointestinal reflexes**

- Integrated completely within the enteric system and controls
  - Secretion, peristalsis, local mixing
- Gut-sympathetic ganglia-gut
  - Gastrocolic reflex
    - Promotes colon evacuation
  - Enterogastric reflex
    - Prevents stomach motility and emptying
  - Colonoileal reflex
    - Inhibits ileal emptying
- Gut-spinal cord / brain-gut
  - Uses vagus nerve
  - From stomach and duodenum
    - Controls gastric motor and secretory activity
  - Pain reflexes
    - Inhibits gastrointestinal activity
  - Defecation reflex
    - Promotes colonic rectal and abdominal contraction

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Figure 1-26. Neurotransmitters involved in regulation of gastrointestinal activity

Figure 1-27. Reflexes of the gastrointestinal tract
duodenum and upper jejunum. To this end, the mucosa releases a compound known as gastric inhibitory polypeptide which slows down the rate of stomach emptying.

**Endocrine control of motility**

- **Cholecystokinin**
  - Is secreted by I cells of the mucosa of the duodenum and jejunum
  - Responds to FA, monoglycerides in intestinal content
  - Increases contractility of the gallbladder
    - Secretes bile into the small intestine
    - Emulsifies fat
  - Inhibits stomach motility
  - Slows down transit

- **Gastric inhibitory polypeptide**
  - Is secreted by mucosa of upper intestine
  - Responds to fat and protein
  - Slows down stomach emptying
  - Allows for proper digestion of intestinal content

**Figure 1-28. Hormones influencing motility of different components of the GIT**

**Figure 1-29. Relative particle size distribution within the stomach**

**Figure 1-30. Sequential movements of a primate's stomach that permits the mixing of ingesta and advancement of digested materials towards the duodenum**

**Functional movements within the GIT.** The stomach carries out a significant amount of movement in order to mix its content and to separate physically large particles into smaller portions. As the food enters the stomach, it starts forming layers, with the deepest layers being the smaller particles, ready to be emptied into the duodenum, and those close to the esophagus being the larger particles which need significant disintegration before moving to lower layers (Fig. 1-29).
Acid and/or enzymes do most of the digestion chemically, but the movements of the stomach significantly support this process. These movements are performed in a repetitive manner following a similar pattern. This pattern changes from species to species, and depends on the specific anatomical design of the organ. Figure 1-30 depicts a stomach’s pattern of movement.

The stomach has significant movement to mix and initially digest the ingesta. In order to properly digest the food and discard what is indigestible, the GIT has to move the intestinal contents along the tract, but at the same time, provide opportunity for proper digestion. To achieve this, there are two types of movements within the GIT, the propulsive and the mixing movements (Fig. 1-31). Propulsive movements push contents along the tract which are also implemented by a coordinated effort of longitudinal and circular muscles of the gut (Fig. 1-32).

The rate at which the contents are moved influences the degree of digestion taking place, with a longer retention resulting in a more thorough digestion process.

Propulsive movements take place in waves in which consecutive sections of the intestine reduce their diameter forcing the intestinal contents towards the anus.

Mixing movements do not displace food along the tract. They consist of the constriction of relatively close sections of the intestine forcing a change in position of the content, as well as to facilitate physical separation and disintegration of particles so that they are better exposed to digestive enzymes (Fig. 1-33).