Digestive system

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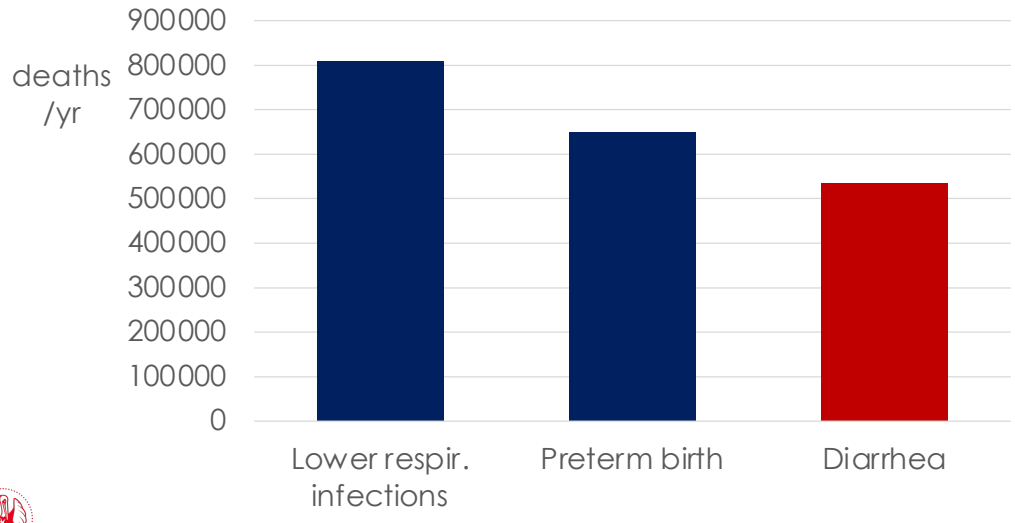
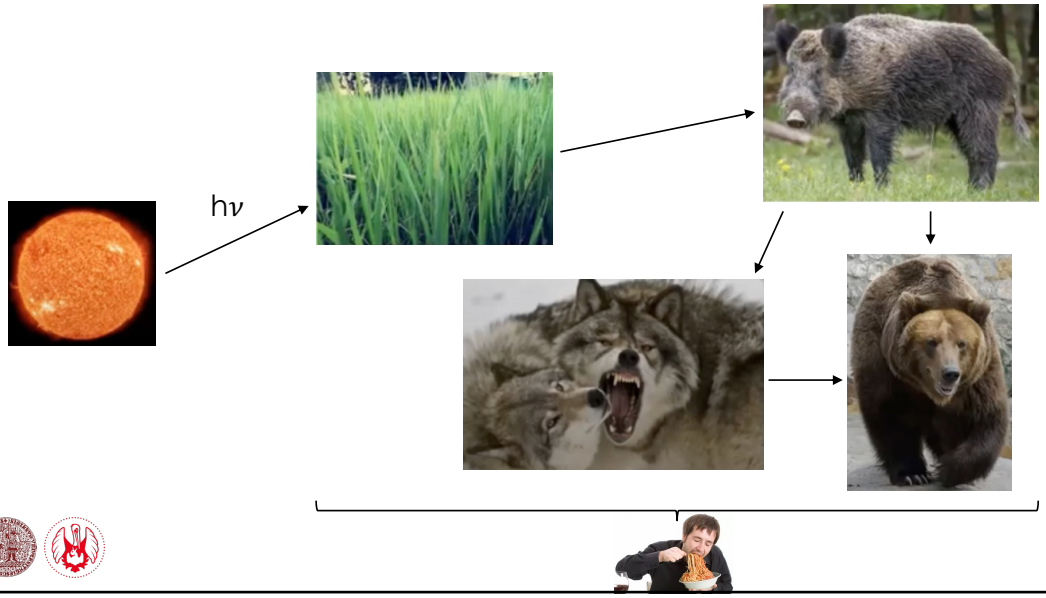
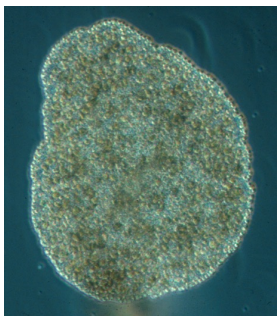
Causes of death: children ≤5 yr



All life depends on external energy

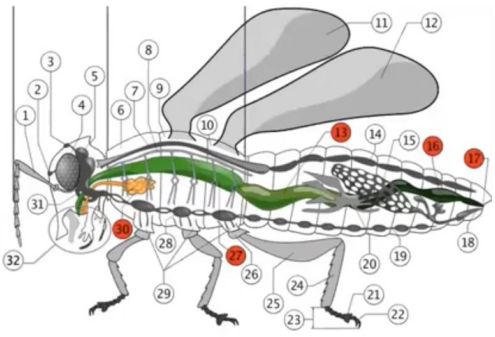


Evolution



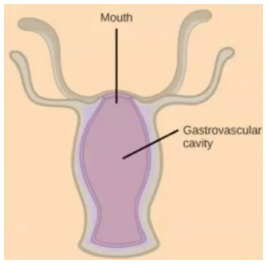
Placozoa

X



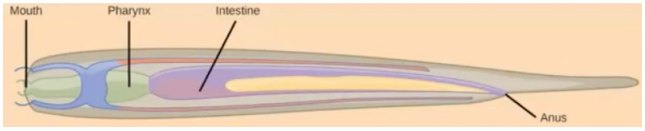
epithelial cells lining an inner lumen

Evolution



- gastrovascular cavity
  (e.g. coral, jelly fish, sea anemones)

- alimentary canal



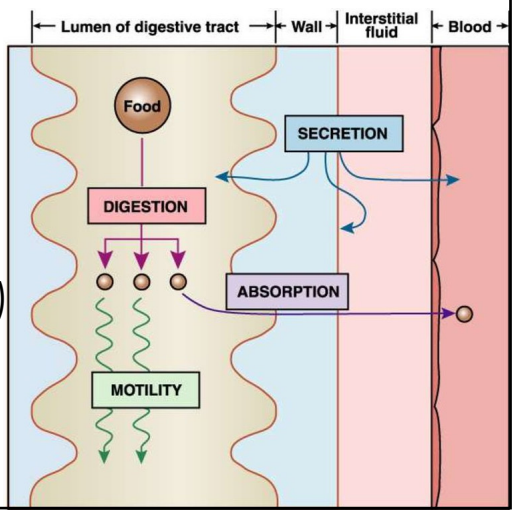
Evolution

- phagocytosis + <u>intracellular digestion</u>: most common

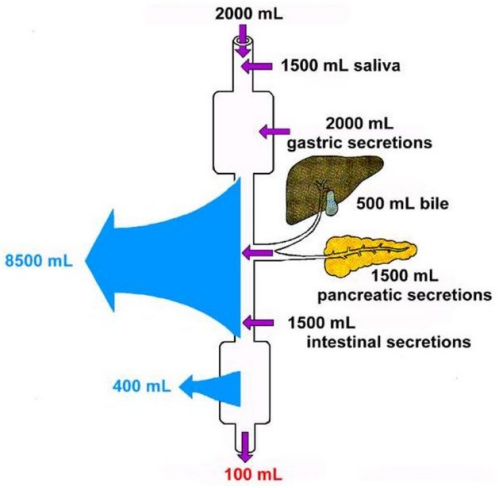
- <u>extracellular digestion</u> + absorption of smaller molecules:
  only vertebrates & most insects

Components of food intake

- movement (mouth → anus)
- within that, 2 processes:
  - secretion (→ *extracellular digestion*)
  - absorption (→ *intracellular digestion*)

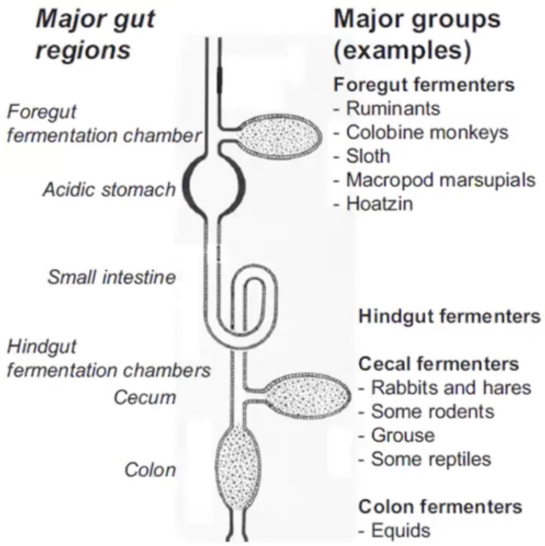


Secretion



- H_2O (enzymes work in solution)
- ions (movement of H_2O, sometimes also of nutrients)
- proteins (enzymes, mucin)
- signaling molecules

Help from microorganisms



Integrated response to meal: phases

- cephalic & oral
- esophageal
- gastric
- small intestinal
- colonic

Cephalic phase

- stimuli:
  - cognitive
    - anticipation, thinking, talking,...
  - olfactory
  - visual
  - auditory

Oral phase

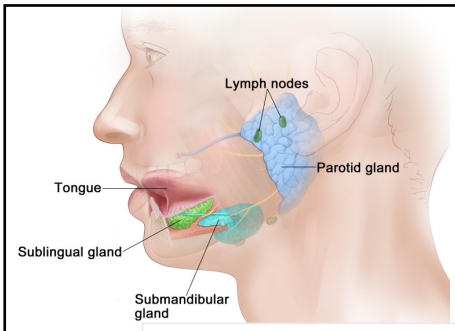
- stimuli:
  - mechanical in mouth
  - taste

Cephalic & oral phase

- parasympathetic activation:
  - ↑ saliva secretion
  - ↑ gastric acid secretion
  - ↑ pancreatic enzymes secretion
  - gallbladder contraction
  - sphincter of Oddi relaxation

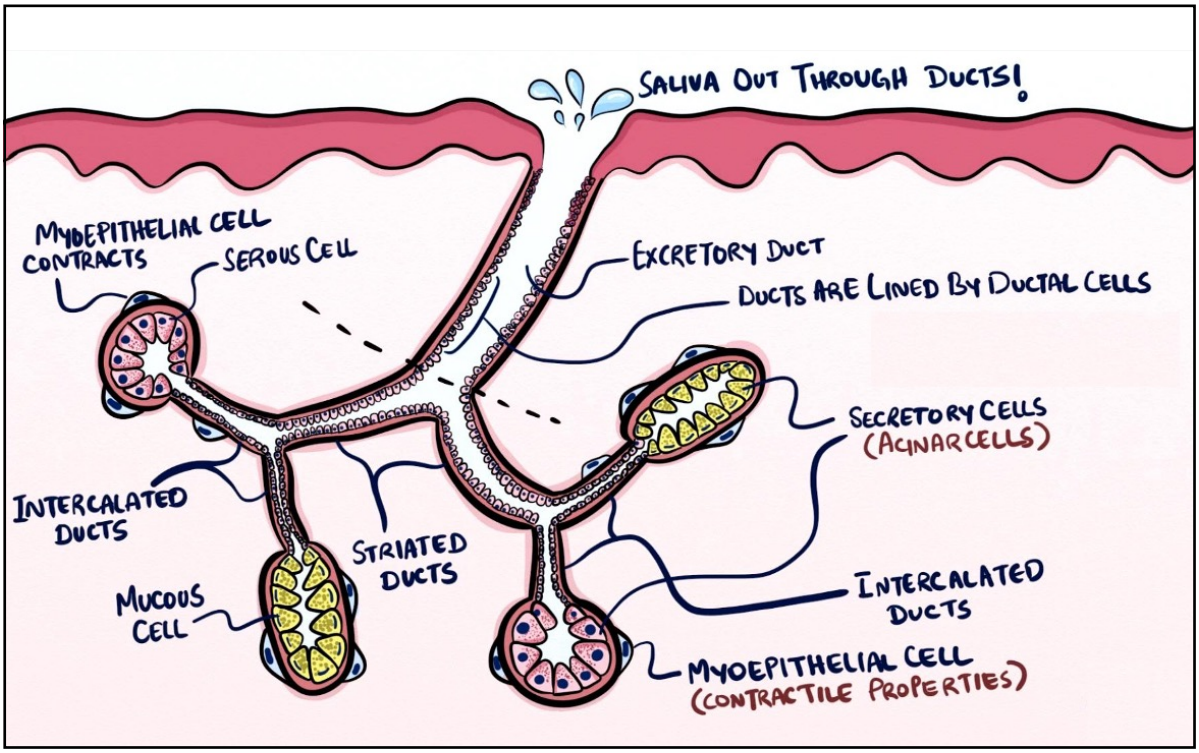
Mouth

- mastication
- saliva
  - lubrication (mucus)
  - solubilization for taste
  - amylase (starch)
  - antibacterial
- lingual lipase
- minimal absorption (alcohol, some drugs)

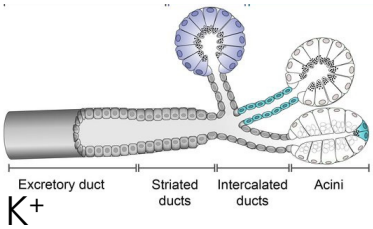


Salivary glands

	serous	mixed	mucous
parotid	■		
sublingual			■
submandibular		■	
small in mouth		■	



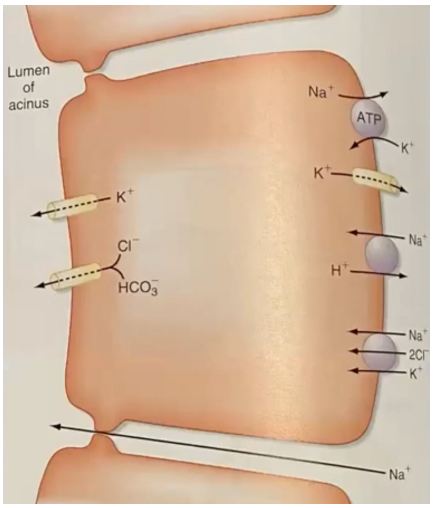
Saliva



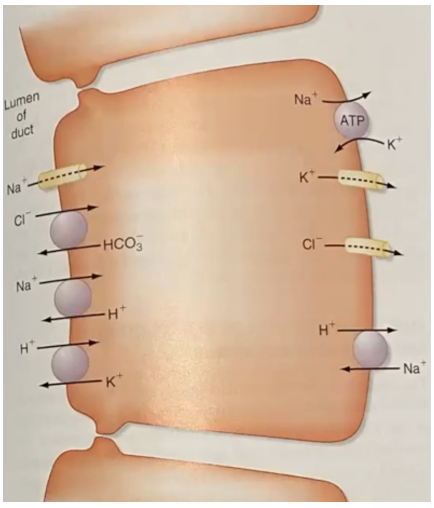
- large flow rate relative to size
- hypotonic, alkaline (pH≤8), high K^+
  - primary secretion isotonic (driven by apical Cl^- channels ⟶ osmotic & el. gradient ⟶ Na^+ & H_2O follow paracellularly)
  - duct cells reabsorb Na^+ & Cl^- & secrete K^+ & HCO_3^- (CFTR)
- amylase, lipase, mucin (glycoproteins), lysozyme (antibacterial)
- growth factors (GIT lining maintenance)

Saliva secretion

acinar cell



ductal cell



Regulation of salivation

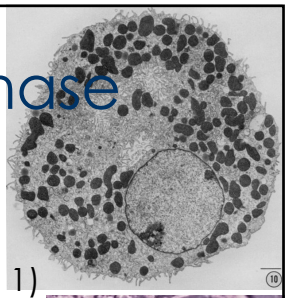
- parasympathicus:
  - main after a meal
  - ↑ secretion of amylase & mucin
  - ↑ transport in ducts

→ more saliva

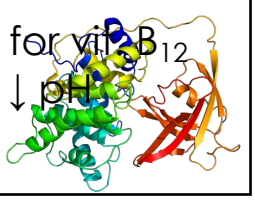
- sympathicus
  - ↑ protein secretion

→ *sticky mouth*

Response to meal: Gastric phase

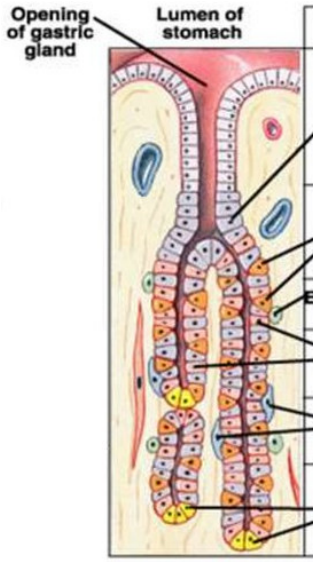


- stomach = strange organ
  - full of strong acid (pH 5 to 1)
    - ↑↑ energy demand (10^6 gradient: pH ~7 vs. 1)
    - need to protect itself
  - just to activate pepsin**?** (+denaturing)
    - 20% of protein digestion, not essential
  - protection against microbes from food
    - (not all do mind)
  - <u>intrinsic factor</u> – glycoprotein necessary for vit. B_{12} (cobalamin) absorption in ileum, needs ↓ pH



- grinding, storage

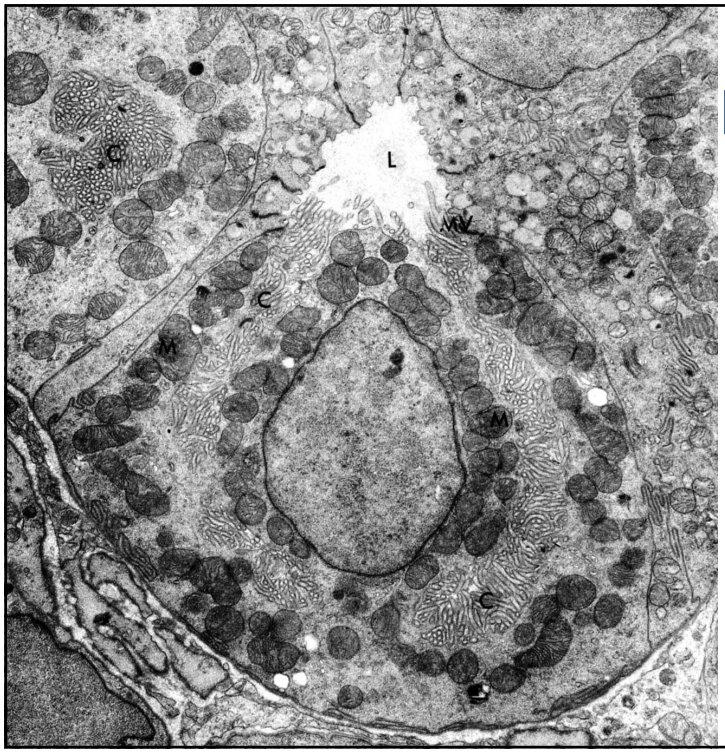
Gastric juice



Source	Substance Secreted	Function
Mucous neck cell	Mucus	Physical barrier between lumen and epithelium
	Bicarbonate	Buffers gastric acid to prevent damage to epithelium
Parietal cells	Gastric acid (HCl)	Activates pepsin; kills bacteria
	Intrinsic factor	Complexes with vitamin B_{12} to permit absorption
Enterochromaffin-like cell	Histamine	Stimulates gastric acid secretion
Chief cells	Pepsin(ogen)	Digests proteins
	Gastric lipase	Digests fats
D cells	Somatostatin	Inhibits gastric acid secretion
G cells	Gastrin	Stimulates gastric acid secretion

Pepsins

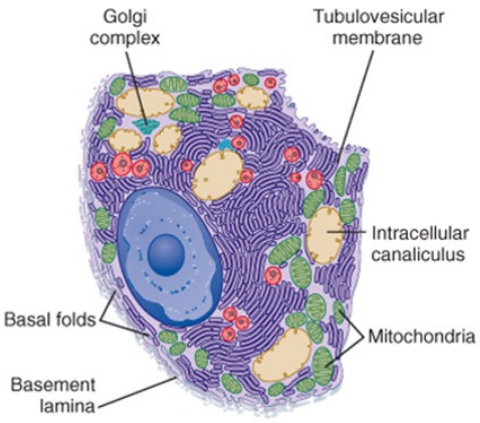
- activation by small N-terminal fragment cleavage
  - only at pH<5, slow at pH 3-5, very fast at pH<3
  - autoactivation
- activity also pH dependent
  - pH optimum = 1.8-3.5 (reversible inactivation at pH>3.5)
  - irreversible inactivation at pH>7.2



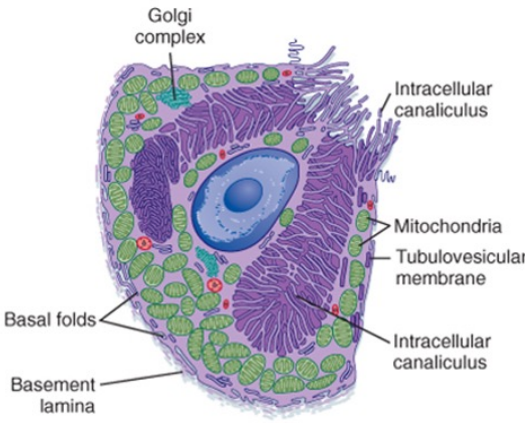
HCl secretion: parietal cells

HCl secretion: parietal cells

rest



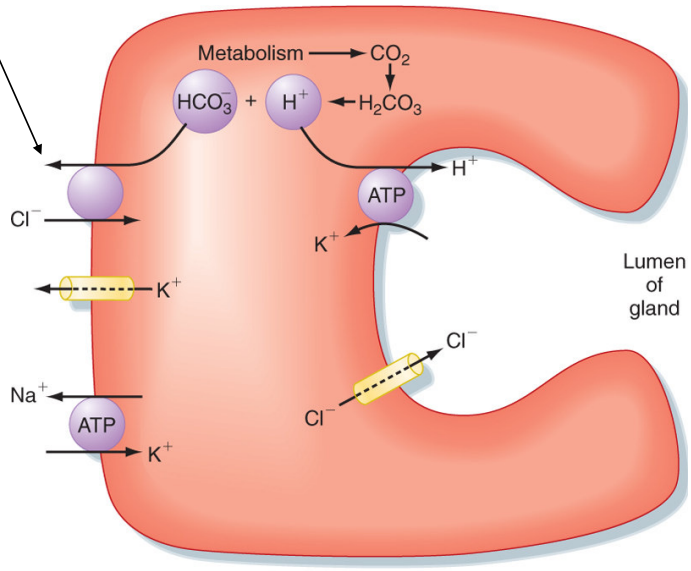
activation



HCl secretion

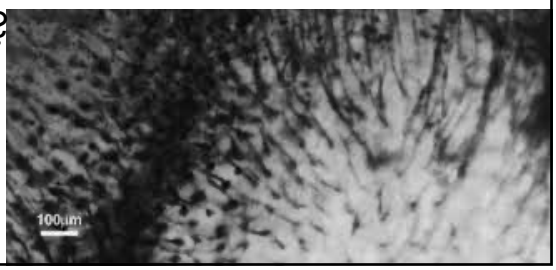
→ high HCO_3^- in blood leaving stomach

- apical H/K antiporter
- basolateral Na/K pump



Protection of mucosa from acid

- continuously renewed mucus layer (~0.2 mm)
  - large glycoproteins – sugars shield the proteineous part
- HCO_3^- secretion underneath mucus (& into it)
- viscous fingering
- protection of glands???



Regulation of gastric secretion

proteins in stomach

cephalic & oral phase

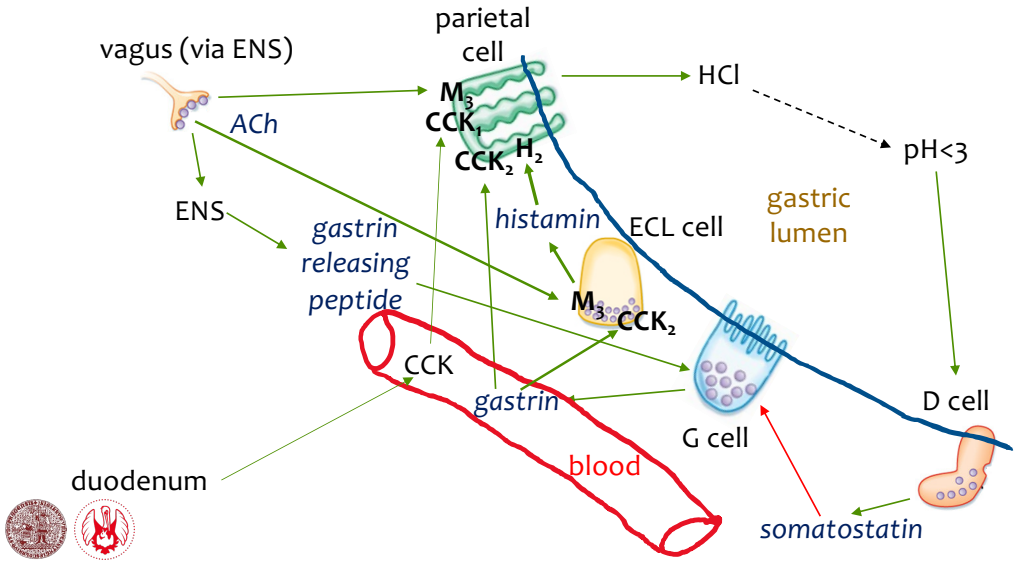
distension

parasympathetic activation (via ENS)

strongest stimulus for HCl secretion,

+ pepsinogen, HCO_3^-, mucus

Regulation of HCl secretion



Other digestion in stomach

- saccharides
  - remnants of amylase activity, negligible
- lipids
  - emulsification (mixing movemer

  - gastric lipase: ~10% of all lipid hydrolysis, not essential

Small intestinal phase

- ↑ pancreatic secretion
- gallbladder contraction
- sphincter of Oddi relaxation
- regulation of gastric emptying
- ↓ gastric HCl secretion
- MMC interruption

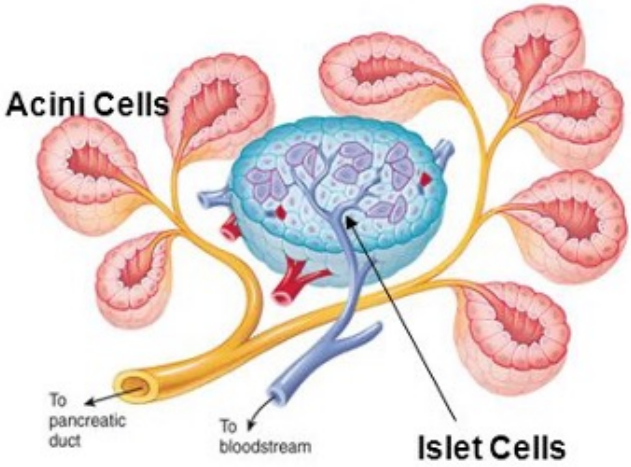
- mechanical & chemical stimuli

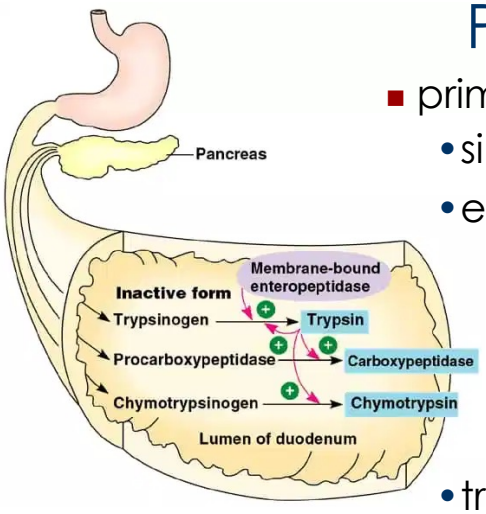
Small intestine

- large internal surface area (~200 m^2)
  - length (5-7 m)
  - villi + crypts
  - microvilli
- pH ~7 (duodenum) to 7.2 (HCO_3^- mainly from pancreas, also duodenal glands)

Pancreas – essential for all digestion

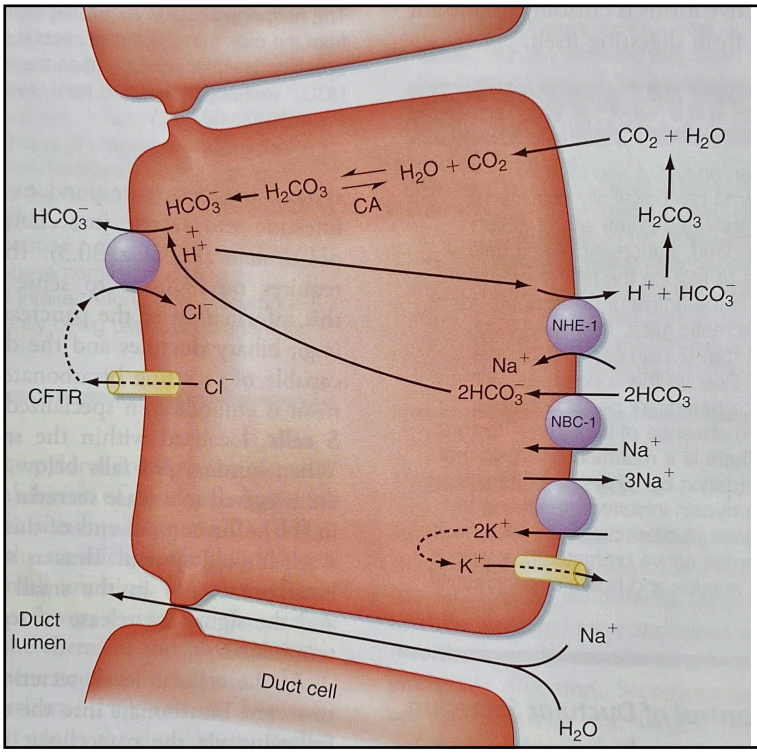
- similar to salivary glands
  - acini
  - ducts
- ~1.5 l/d





Pancreatic secretion

- primary:
  - similar ions as in plasma
  - enzymes (all inactive):
    - trypsin, chymotrypsin, proelastase, procarboxypeptidase A & B
    - amylase
    - lipase
    - (deoxy)ribonuclease
  - trypsin inhibitors (trypsin activates all)
- ducts: H_2O, HCO_3^- (exchange for Cl^-)



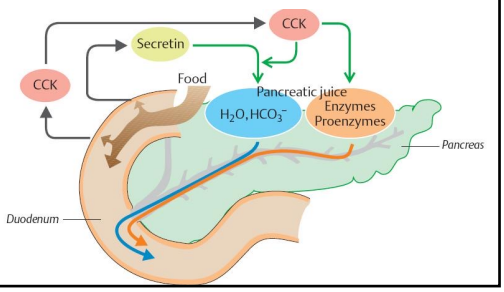
Pancreatic duct cell

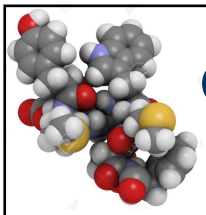
- extra HCO_{3-} in blood from stomach
- carboanhydrase
- NBC1 = Na/HCO_3^- symporter 1
- NHE1 = Na/H exchanger 1

Regulation of pancreatic secretion

presence in duodenum:	duodenal hormone:	secretion in pancreas:
acidity	secretin (S cells)	HCO_3^-
peptides (aminoacids) lipids (free fatty acids)	CCK (I cells)	enzymes

vagus





Cholecystokinin (pancreozymin)

CCK-releasing peptide (parakrinně)

vagus (cefalická fáze)

aminokyseliny

FFA

ENS

monitor peptide (z acinových buněk)

trypsin

enteroendokrinní I buňky v epitelu tenkého střeva (hl. duodenum & jejunum; též ENS)

CCK

↓ vyprazdňování žaludku

CCK_1 receptory

↑ tvorba žluči

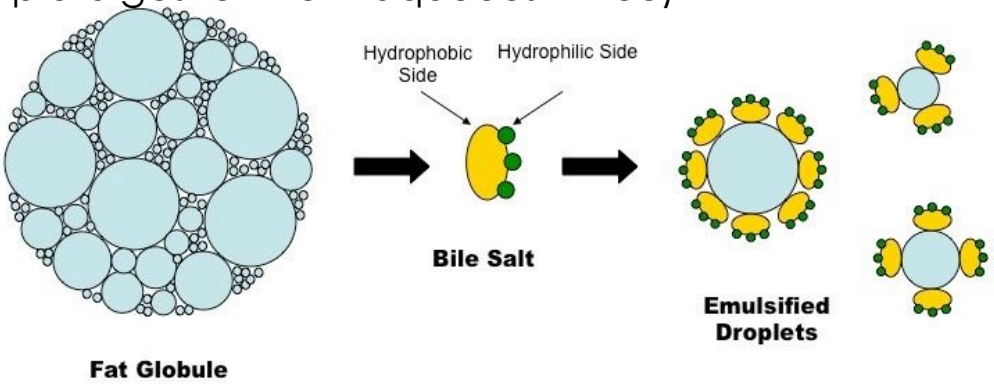
kontrakce žlučníku

relaxace Oddiho svěrače

potlačení hladu

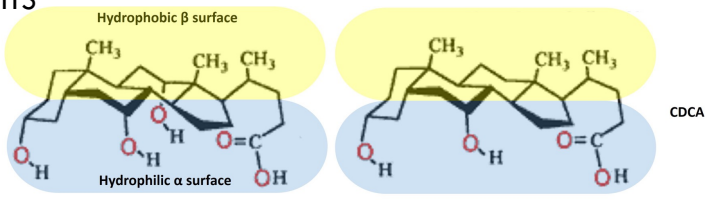
Bile (gall)

- produced in liver
- emulsification of lipids (bile acids [detergents] ⟶ salts ⟶ micelles (shield hydrophobic products of lipid digestion from aqueous milieu)

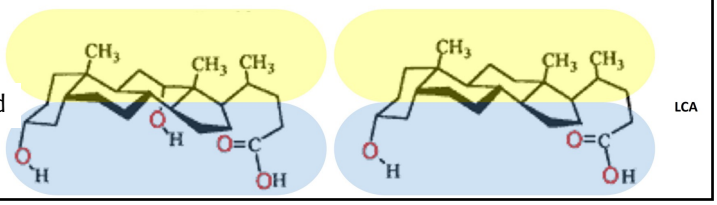


Bile acids (steroid)

- toxic to many bacteria
- conjugated (in liver) with taurine or glycine ⟶ soluble bile salts

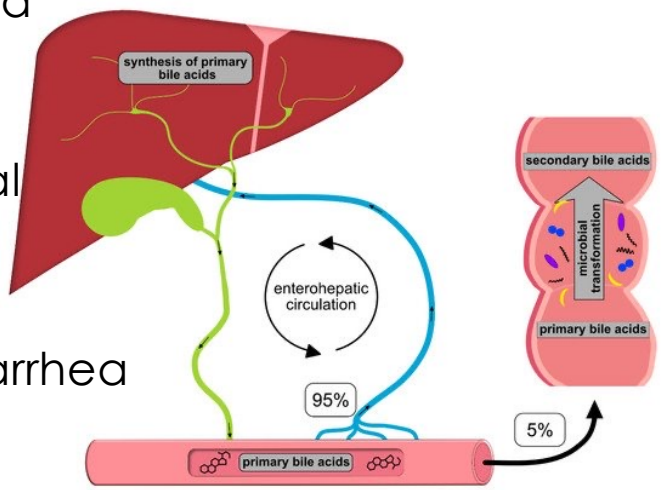


- deconjugated by bacteria



Enterohepatic circulation of bile acids

- recyclation of lipid xenobiotics
- minimal overflow to colon & arterial blood
- 3-4x/d
- dyfunction ⟶ diarrhea



Small intestine enzymes

dipeptides —*dipeptidases*→ amino acids

maltose —*maltase*→ glucose + glucose

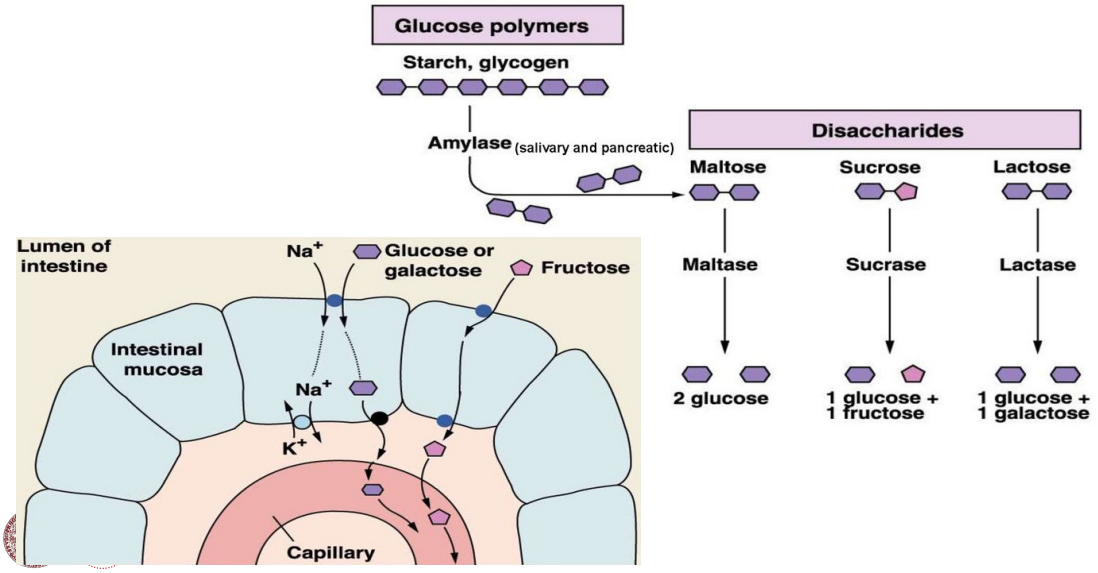
lactose —*lactase*→ glucose + galactose

sucrose —*sucrase*→ glucose + fructose

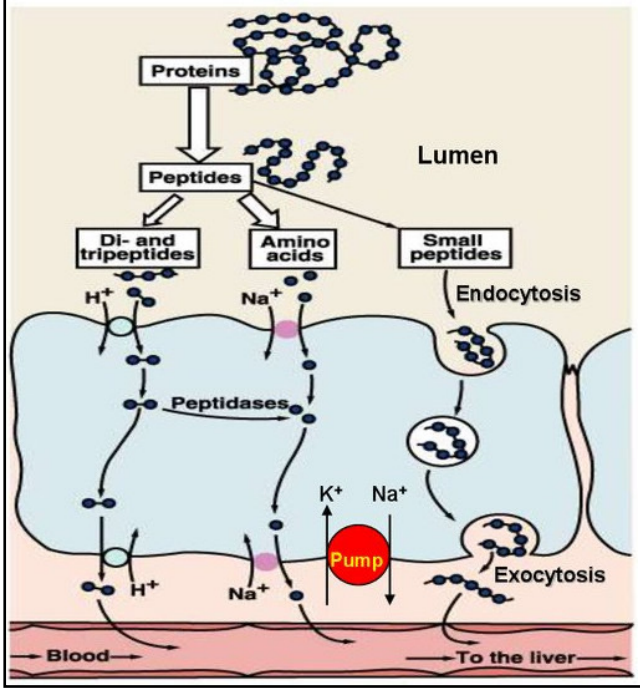
di- & monoglycerides —*lipases*→ fatty acids + glycerol

nucleotides —*nucleotidases*→ nucleosides —*nucleosidases*→ sugars + bases

Carbohydrate assimilation

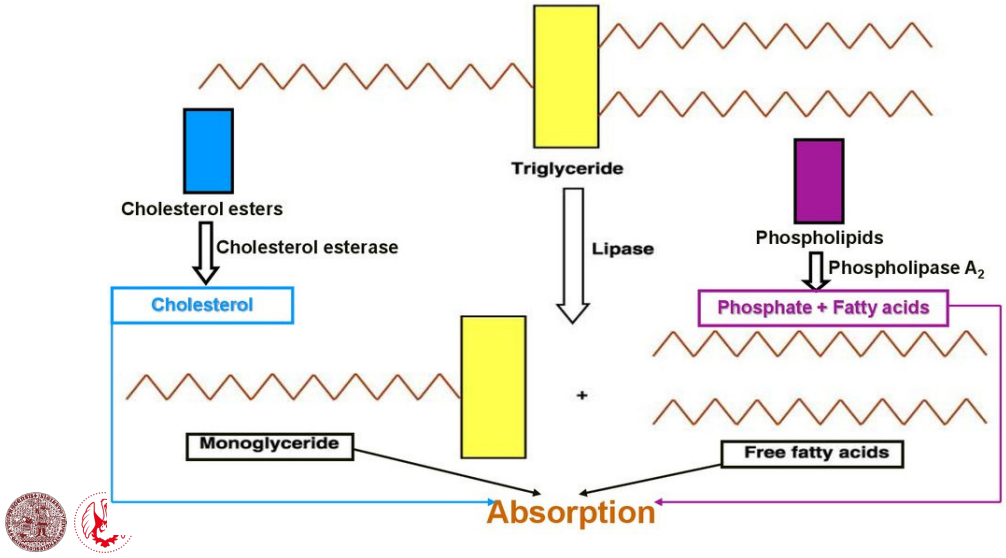


Protein assimilation

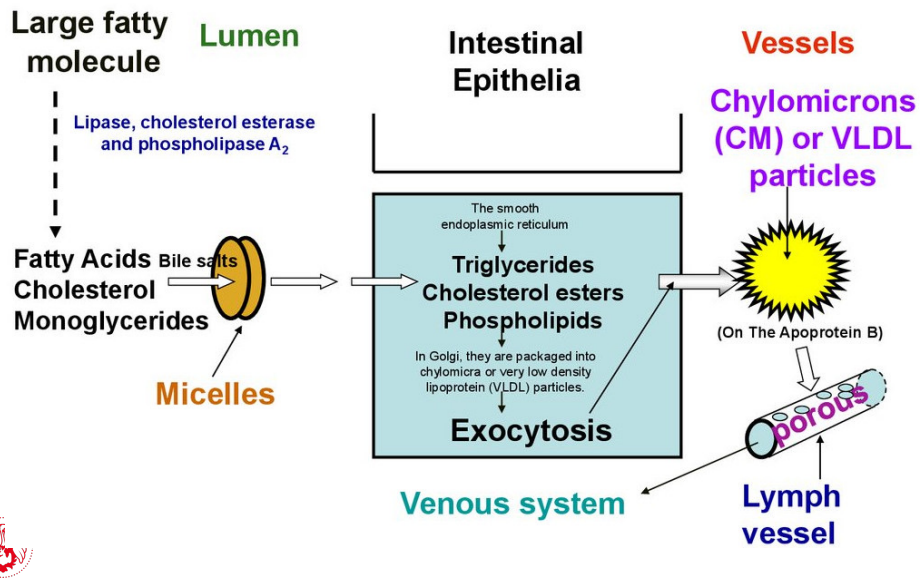


- some small proteins by endocytosis
- AA & di- & tripeptides by Na-dependent secondary active transport

Lipid assimilation



Lipids



Large intestine

- HCO_3^- - neutralization of acids formed by the intestinal flora
- mucus - protection, lubrication
- absorption of vitamins B & K made by bacteria in colon

Satiety

- distension inhibits intake
  ↓ stomach size (bariatric surgery) ⟶ ↓ meal size
- cholecystokinin = satiety hormone
  - ↑ by nutrients
  - inhibits food intake (CCK receptors v CNS)
- glucagon-like peptide 1 (GLP-1)
- peptide YY (PYY)

GIT motility

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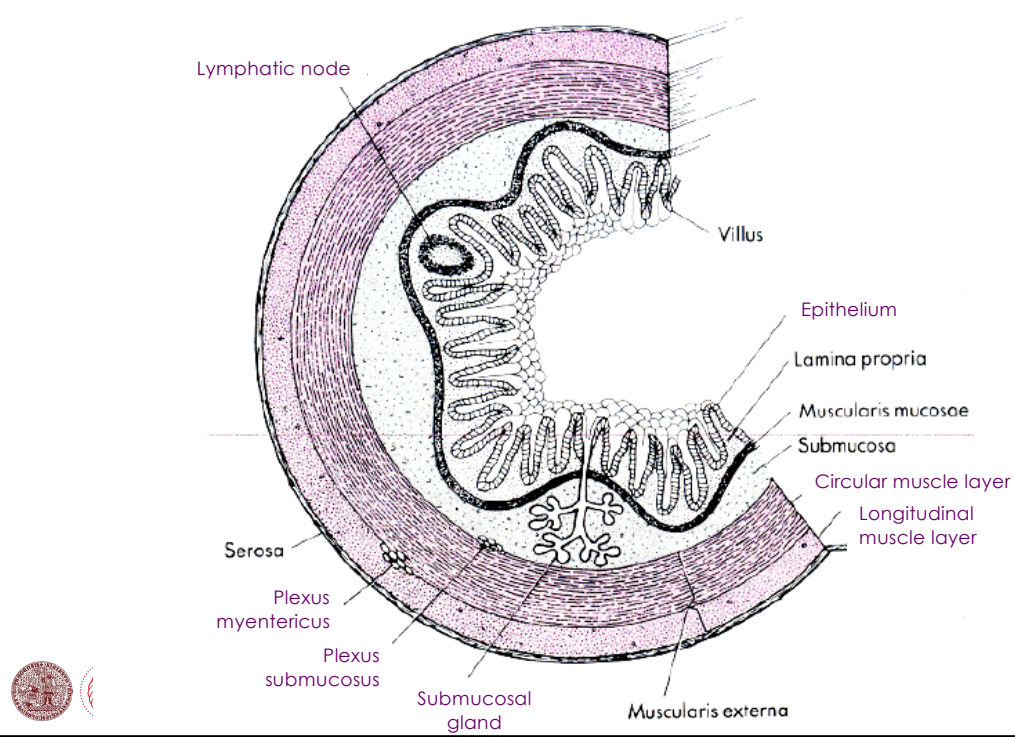
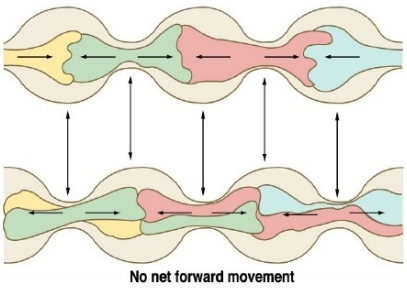
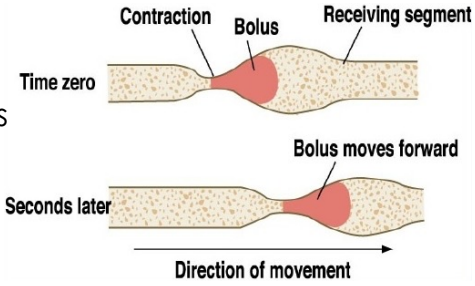


Types of GIT movements



1. Mixing

2. Peristalsis



3. Reservoir

Regulation of motility

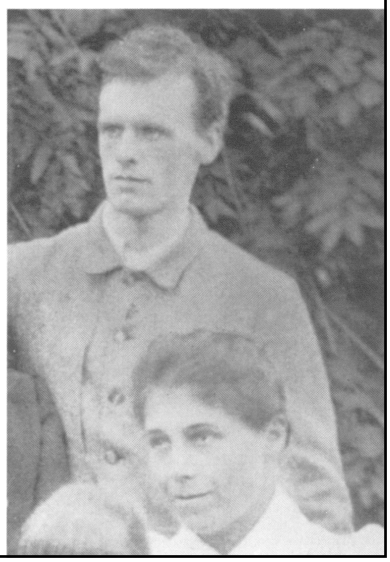
- nerves
  - **enteric nervous system (ENS)**
  - parasympaticus, sympaticus
  - partly also somatic motoneurons
- hormones
  - made in GIT
    - gastrin, secretin, cholecystokinin, motilin,...
  - partly also other
    - e.g. glucocorticoids & catecholamines in stress

Regulation of motility

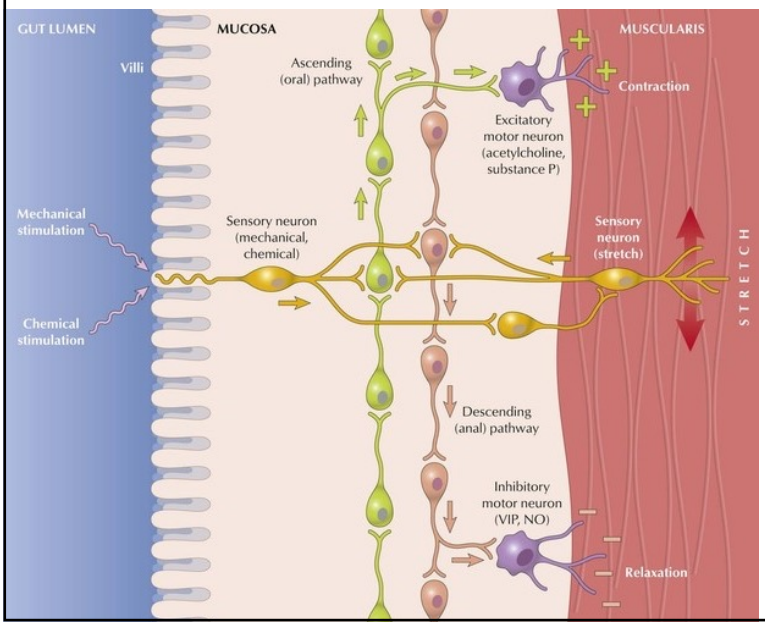
- mediators of the GI immune system
  - has at least as many cells as the immune system of the rest of the body
- mast cells
- histamine, PGs, LTs, cytokines,...

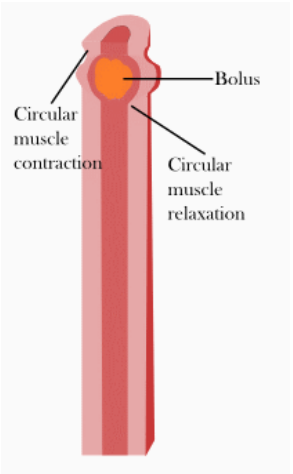
ENTERIC NERVOUS SYSTEM

- Anatomy 19. century ~ relay ganglia
- Bayliss, Starling 1899:
  peristaltic reflex,
  persists after denervation
  other organs are stopped by denervation
- Today:
  - ENS: autonomous, complex system
  - "neurogastroenterology"



Peristaltic reflex





Enteric nervous system (ENS)

- Governs many GIT functions without external inervation (modulation only)
  - motility
  - secretion
  - collaboration with immune system on defense
  - growth regulation

ENS

- ~10^8 neurons
  - $^1/_{1000}$ brain
  - > spinal cord
- no distinct neuromuscular junctions (nerve endings freely distributed among SMC)
- innervates also vessels (mainly vasodilation) & surrounding organs (bladder, pancreas)
- perhaps phylogenetically older than CNS (food needed before locomotion)

ENS & CNS: similarities

- Glial instead of Schwann cells (similar to astrocytes in CNS)
- All neurotransmitters so far known in CNS:
  - excitatory motoneurons: mainly ACh (muscarinic receptors on SMC)
  - inhibitory motoneurons: VIP & NO
  - interneurons: mainly ACh (nicotinic receptors on target neurons) & GABA
  - serotonin (5-HT; 95 % of all)

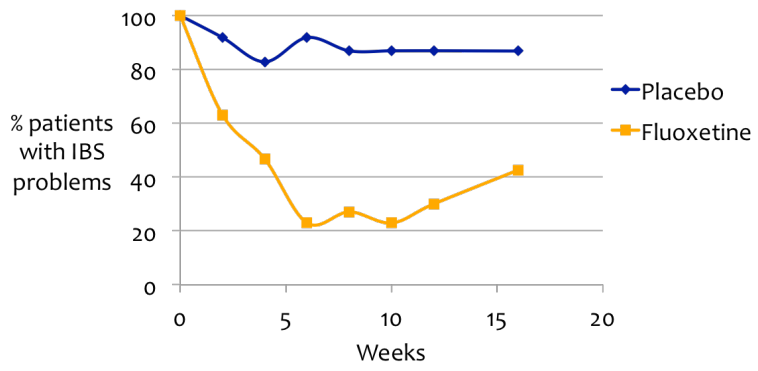
ENS & CNS: similarities

Similar sensitivity to toxins, drugs, diseases

- Antidepressants: ↓ 5-HT re-uptake in brain & ENS - nausea, diarrhea, then constipation (desensitization)
  - can be used to "calm down" GIT (ENS more sensitive than CNS)
- Lewy's bodies (Parkinson's disease), amyloid plaques & neurofibrilar clusters (Alzheimer's disease) also in the gut (diagnosis by rectal biopsy?)
- Therefore: GI & psychic problems often co-exist

Antidepressant fluoxetine (Prozac)

Selective serotonin reuptake inhibitor (SSRI)



VAHEDI et al: *Aliment. Pharmacol. Therap.* 2005

ENS & CNS: similarities

Can learn

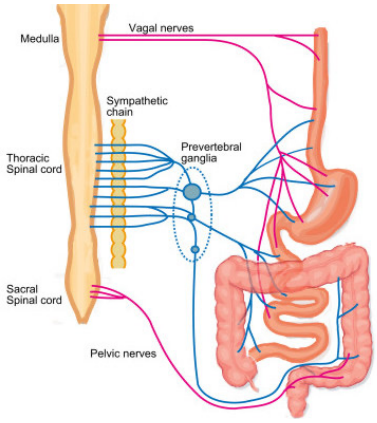
- Hirschsprung's disease - genetically determined absence of nerves in the most distal GIT part - inability to defecate
- within 18 months after resection of the defect, the more proximal part "learns" to defecate (it couldn't do it at the beginning)

ENS & CNS: communication

- ~10x more AP ENS → CNS than CNS → ENS
- e.g. gastric ulcers:
  - history: psychosomatic ("soul" → GI)
  - today: vice versa - *Helicobacter pylori* is primary, psychic discomfort follows ENS irritation (GI → "soul")
- afferentation from ENS to CNS can act anti-depressively, support learning (c.f. mood when hungry vs. after a good meal)

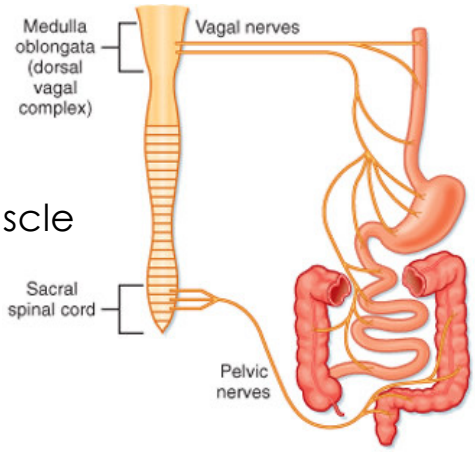
Vegetative innervation

- Mainly co-ordination of remote parts
  - e.g. gastrocolic reflex: stomach filling → ↑ colon act
- Parasympathicus
- Sympathicus



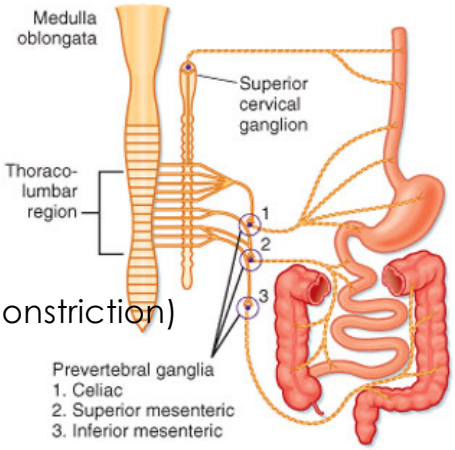
Vegetative innervation: Parasympathicus

- Down to the transverse colon: vagus branches; the rest: pelvic nerves
- Preganglionic, mostly cholinergic fibers
- Innervates ENS neurons, not the intestinal smooth muscle
- Mostly ↑ motility & secretion



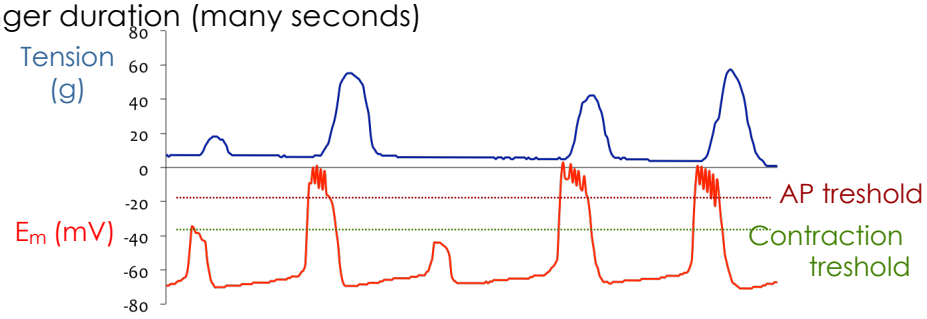
Vegetative innervation: Sympathicus

- Postganglionic adrenergic fibers from prevertebral & paravertebral ganglia
- Does not innervate intestinal smooth muscle, rather
  - ENS neurons; they mediate the influence on muscles
  - glandulae
  - vascular smooth muscle (vasoconstriction)
- Usually ↓ motility;
  ↑ tone of some sphincters

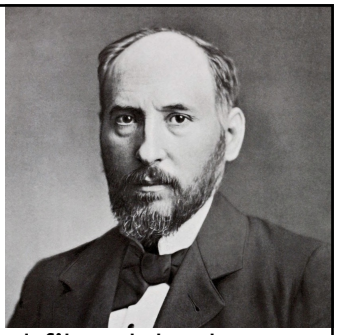


Slow E_m waves in SMC (basal electric rhytm, BER)

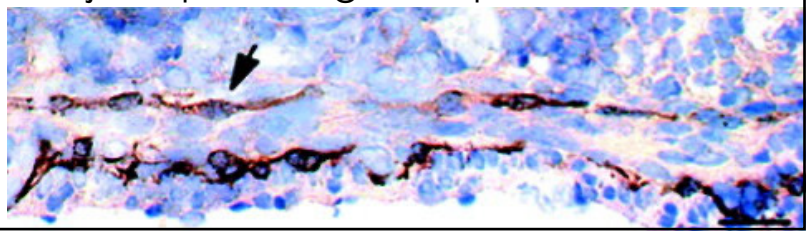
- ~3/min in stomach, 12/min in duodenum
- easily spreads through el. connections → GIT segments synchro
- BER differs from spontaneous activity in heart etc.:
  - lower frequency (max ~40/min, typically 3-12/min)
  - lower amplitude (do not overshoot over 0 mV)
  - longer duration (many seconds)



BER is generated by interstitial cells (of Cajal)

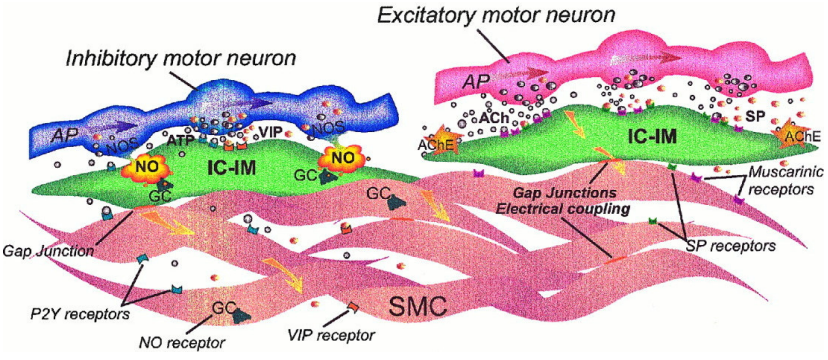


- Between the 2 layers of musculature
- Properties of both smooth muscle and fibroblasts
- Gap junctions with muscles of both layers and other cells of Cajal - spreading of depolarization



Interstitial cells (of Cajal)

- Tight synapses with neurons (mediate ENS influence on muscles)
- Separated activity of different GIT parts: discontinuity of the interstitial cells



Chewing (mastication)

- Conscious & unconscious (lighter phases of sleep)
- Function:
  - small pieces (5-15 ml) from large
  - lubrication
  - amylase (starts breakdown of starch)
- Can generate enormous force (50-80 kg on molars)
- In humans nutrition not endangered even with substantial reduction of chewing area

Swallowing: structure of the reflex

- afferent branch: tactile receptors mainly in entry to pharynx
- swallowing center in medulla & lower pont
  - easily impaired in CNS injury (stroke,...)
- efferent branch:
  - head nerves to pharynx and upper esophagus
  - vagus to rest of esophagus
  - to respiratory center
- but vagus X evokes alternative ways of peristalsis (ENS, myogenic mechanisms)

Swallowing: oral phase

- conscious
- or (more often) reflex pharynx stimulation by saliva or food (~ 1000x/day, incl. sleep)
- tongue moves food to upper pharynx by pressing against hard palate

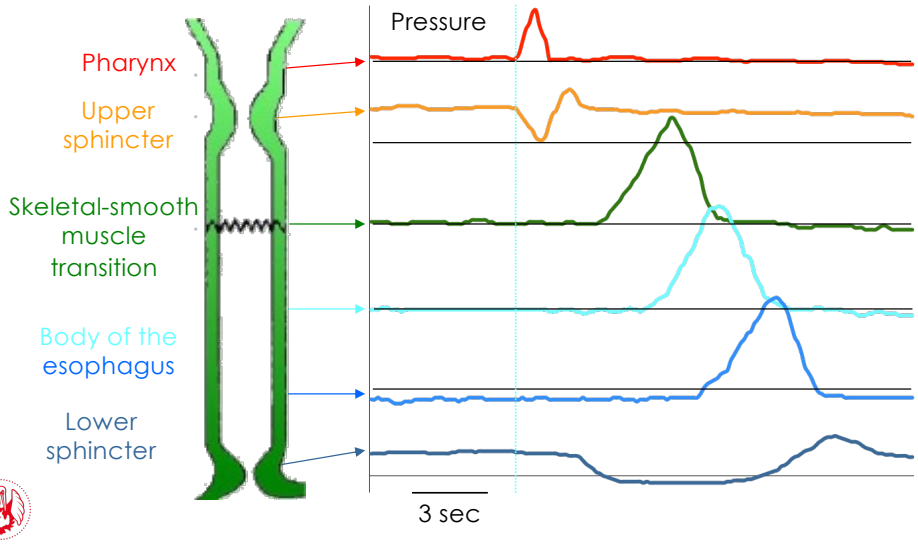
Swallowing: pharyngeal phase

- <1 sec
- reflex, activation by mech. stimulation
- soft palate ↑, closes entry to nose
- vocal cords close, larynx ↑ (epiglottis closure)
- ↓ breathing
- short relaxation of upper esophageal sphincter (reflex opening after food passage)
- contraction of upper esophagus (skeletal muscle)
- peristaltic wave initiation

Swallowing: esophageal phase

- upper ~1/3 of esophagus = skeletal muscle (longitudinal & circular layer)
- then "gradient" skeletal → smooth
- last ~1/3 = smooth muscle
- skeletal & smooth: innervation by vagus
  - in skeletal muscle part, vagus fibres end by neuromuscular plates (myenteric plexus only sensoric function)
  - in smooth muscle part, vagus fibres end at ENS neurons
- primary peristaltic wave 3-4 cm/s (6-8 s)

Swallowing: esophageal phase



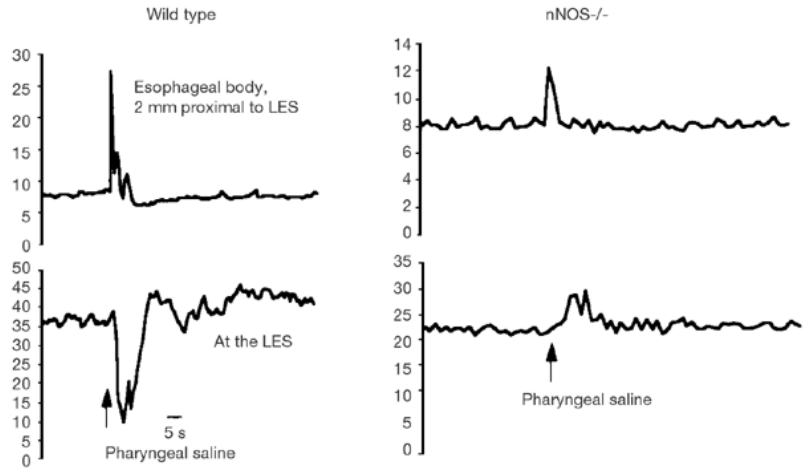
Secondary peristaltic wave

- if primary not successful
- not full swallowing reflex
- only esophageal afferents
- peristaltic activity restricted to esophagus
- no pharyngeal contraction, no UES relaxation
- local reflex similar to peristaltic reflex in the intestine
  - distention of esophagus → activation of local sensory nerves → contraction above the distention and relaxation below it

Esophageal reflux

- lower sphincter sometimes opens even without swallowing (~ physiological reflux)
- if too much → esophagitis ("burning")
- pressure in esophagus ~ thoracic < abdominal
  - used for measuring intrapleural pressure
  - promotes reflux
- esophagus crosses the diaphragm at the level of the lower sphincter → diaphragm contraction helps to close the sphincter - does not work in diaphragmatic hernia

Lower esophageal sphincter is nNOS-dependent



Stomach - structure

- circular muscles thickens towards the antrum
- longitudinal essentially missing in the upper 1/3
- oblique only the lower 1/2

Stomach - functions

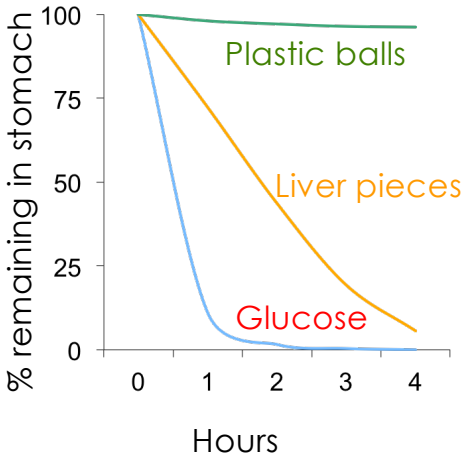
- reservoir
- grinding
- mixing with stomach secretion
- **continuous filling of the gut**

Stomach - reservoir

- mainly fundus & body
  - weak or no contractions - minimal mixing for a long time
  - thin muscular layer
- empty volume 50 ml, pressure ~ 5 mmHg
- volume can ↑ to ~ 4 l
- pressure ↑ only when volume ↑ by >1-1.5 l
  - receptive relaxation
    (vago-vagal reflex, i.e. afferentation from stretch receptors through vagus to CNS [~same area as swallowing], efferentation to SMC also through vagus)

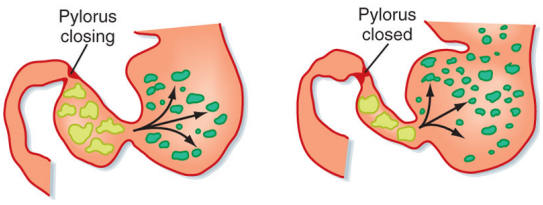
Stomach - reservoir

- chymus settles to layers according to density, large pieces leave the last
- lipids form film on surface ⟶ digested last
- fluids "by-pass"



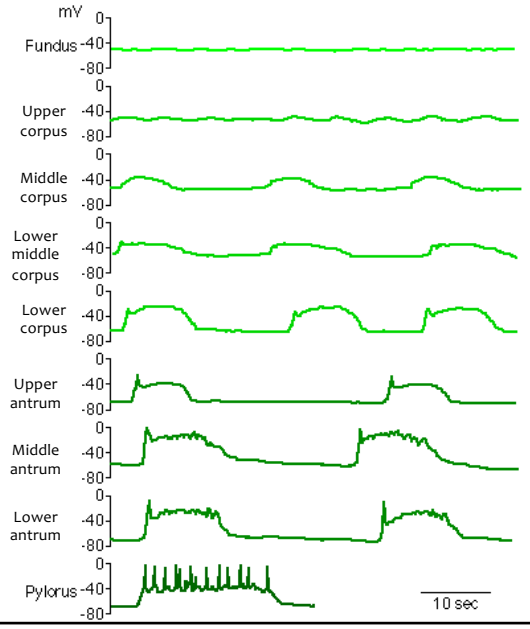
Stomach – grinding, mixing with digestive fluids

- antrum peristalsis
  - starts near central body (cluster of interstitial cells)
  - stronger & faster towards antrum
- retropulsis
  - strong contractions of antrum against the direction of peristaltic wave
  - presses chyme back to stomach through narrow hole created by the peristaltic wave



Electrical activity of the stomach

- slow waves (BER) spread from pacemaker zone ~ middle corpus
- BER ↑ towards antrum
- only in antrum BER amplitude > threshold for AP
- shape similar to AP in heart but 10x longer



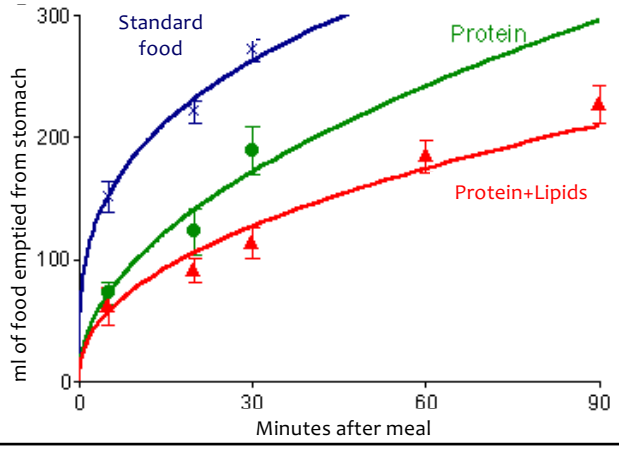
Stomach - filling the gut

- continuous processing by duodenum (despite irregular pattern of food intake)
- prevents injury to duodenum by acid
- strong contractions of antrum (strong muscles, middle oblique layer) against almost closed pylorus (prevents regurgitation - bile could damage stomach wall)
- stomach empties in ~ 3 hours

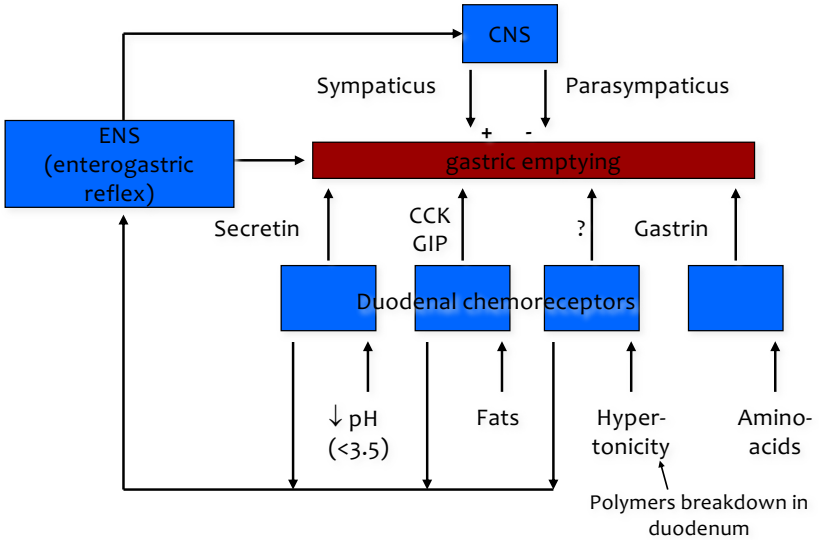
Stomach emptying depends on food composition

Intestine digests different nutritients at varying rates.
This "dictates" the rate at which it is filled

That 's why fats help prevent drunkeness: fat stays longer in the stomach, keeps alcohol there, alcohol resorption from stomach is slower than from gut

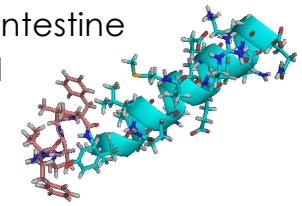


Regulation of stomach emptying



Migrating myoelectric complex (MMC)

- empty stomach rests ~75-90 min, then 5-10 min intense contractions of antrum with relaxed pylorus
- removes non-digested remnants (even large pieces)
- stimulated by motilin
  - polypetide (22 AA) hormone from small intestine
  - produced in hunger, perhaps stimulated by high pH in duodenum?



Vomiting (emesis)

- usually preceded with nausea, sometimes anorexia, autonomic reactions (salivation, sweating, cold skin,...)
- vomiting center in medulla (next to cardiovascular & respiratory centers)
- mechanical stimuli (distension), injury, pain
- stomach/duodenum, larynx entry, inner ear
- emetics (chemoreceptors in stomach/duodenum or bottom of 4th chamber)

Vomiting

- reverse peristalsis from the middle of small intestine to larynx
- forced inspiration against closed glottis - ↓ intrathoracic pressure, ↑ abdominal (diaphragm)
- strong contraction of abdominal muscles & diaphragm
- relaxation, then closure of pylorus, relaxation of LES and finally UES (glottis closure, ↓ breathing)
- protective reflex against toxicity x longer vomiting can cause metabolic alkalosis & dehydration

Small intestine

- duodenum first 5% of length, jejunum next 40, ileum the rest
- most of digestion in duodenum & jejunum, ileum not necessary
- peristalsis simultaneously only in short segments (~10 cm) (except MMC)

Small intestine : segmentation

- alternating localized contractions of circular muscles
- mix chyme with intestinal fluid, contact with intestinal wall
- frequency determined by BER (~11-13/min duodenum, 8-9 end of ileum)
- BER run along the whole length, AP only locally - in these places segmentation contractions
- BER independent of innervation, contractility ↑ by PNS, ↓ by SNS (through ENS)

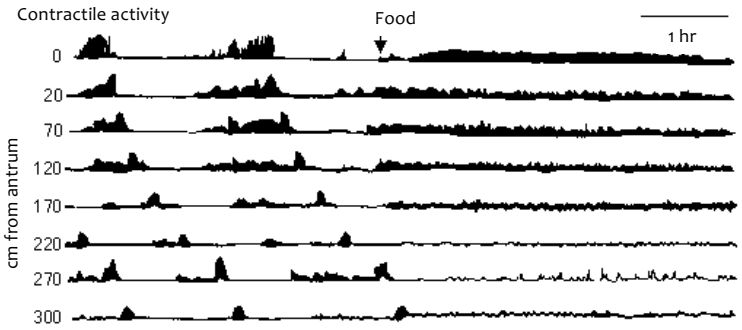
Intestinal reflexes

- local (e.g. peristaltic reflex) - ENS only
- mediated by both ENS & external innervation:
  - intestinointestinal reflex - excessive distension of one part of the gut relaxes the rest
  - gastroileal reflex - ↑ stomach activity → ↑ chymus movement through ileocecal sphincter
  - ileogastric reflex - ↓ stomach motility elicited by distension of ileum

MMC in hunger

- similar as in stomach; gradually from there → end of small intestine
- segmentations cease
- peristaltic waves include ~70 cm of gut
- every 70-90 min, the whole smaller intestine traversed by a series of MMP in 1-2 hr

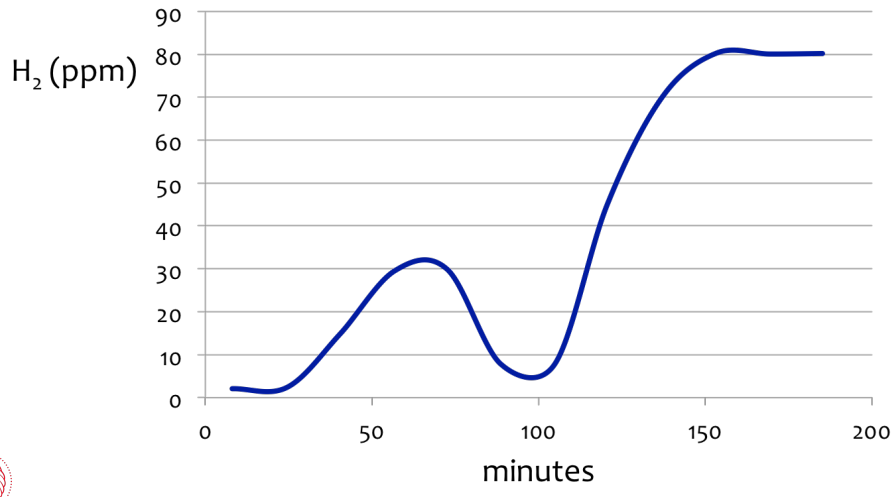
"sweeps" non-digested remnants & prevents bacteria migration from colon



Weak MMC

- bacteria remain in small intestine → they grow (plenty of food)
- they release H_2 (no other source in humans)
  - only when they can use non-digested sugars (normally not present in colon)
  - elevated H_2:
    - either undigested sugar in colon (e.g. lactose intolerance, accelerated passage)
    - or bacteria go upstream to ileum
  - some H_2 gets in blood, from there to breath, can be measured

Breath H_2 test



Contractions of muscularis mucosae

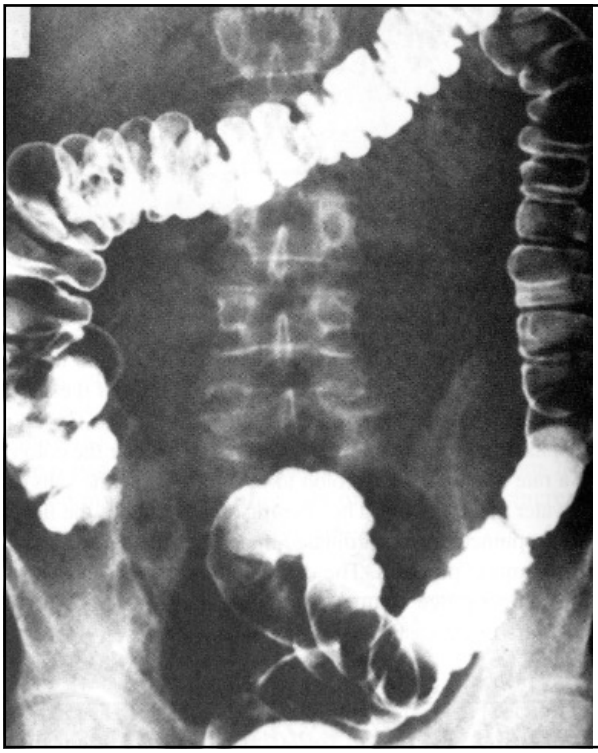
- alter the shape of ridges & folds of mucosa, contract the villi ("milking" of the products of digestion to lymphatic passages), "waving" of the villi
- improve contact of chyme with mucosa, mixing
- support lymph flow

Emptying of ileum

- ileocecal sphincter (valve) normally closed (e.g. because of bacteria)
- opened by distension of end of ileum (local reflex)
- closed by distension of proximal colon (local reflex)

Large intestine

- main functions:
  - H_2O & ions absorbtion (~20 l H_2O/d invested into digestion)
  - storage of useless remnants (typicaly 15-30 hr, but up to 30% can stay here for ~1 wk)
- therefore mainly mixing, only ~5% peristalsis
- mixing more difficult with ↑ density
- haustrations, swing movement, mass movement



Haustrations

- similar to segmentation, but more marked & in anatomicaly pre-defined locations of circular muscle layer
- governed by BER from interstitial cells (~6/min)
- usually no AP
- stronger contractions (e.g. ACh) by prolonging BER

Swing movements of large intestine

- longitudinal muscles, mixing
- controlled by myenteric potential oscillations (lower amplitude, higher frequency than slow waves)
- have APs on their top, APs elicit contractions
- contractions are stronger when APs more frequent (e.g. ACh)

Mass movement

- 1-3x/day (usually after meal)
- wave of strong contraction
- moves content to larger distances (most of colon length)
- colon remains contracted for a while
- overall movement is slow (max 5-10 cm/hr)
- controlled by ENS
- SNS blunts movements, PNS stimulates haustrations of proximal parts & expulsive movements of distal parts

Reflexes of large intestine

- colono-colic - distension of one part relaxes the rest (partly SNS)
- gastro-colic - filling of stomach increases frequency of mass movements (SNS, PNS, CCK, gastrin)
- similarly duodeno-colic

Rectum & anal channel

- Rectum usually (almost) empty (retrograde contractions return content to sigmoideum, until there is too much of it)
- Just before defecation mass movement in sigmoideum fills rectum → ↑ pressure → reflex relaxation of inner sphincter (smooth muscle) & contraction of outer sph. (skeletal muscle controlled intentionally via pudendal nerves)
- Stretch receptors in rectal wall can adapt - urge to defecate can temporarily subside id suppressed

Defecation

- reflex controlled from sacral spinal cord, modulated from higher levels (conscience, will)
- efferent branch - ACh parasympathetic fibers in pelvic nerves
- highly propulsive contraction of descending colon & sigmoideum
- relaxation of both sphincters (outer voluntary)
- inspiration pushes the diaphragm downwards
- contraction of expiratory muscles with full lungs & contraction of abdominal muscles increase abdominal pressure (up to 200 mmHg)