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PERSPECTIVES

From watery and fluffy to soft and formed: What shapes our stool?

Anita Annahazi
and Michael Schemann
Human Biology, Technical University Munich, Freising, Germany
Email: schemann@wzw.tum.de

Edited by: Kim Barrett & Michel Neunlist

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Bowel movements can occur in any shape or form. However, physiologically, they are evacuated as pre-formed pellets or sausages in the case of many mammals, including humans. Any deviations (i.e. too watery or too hard and lumpy stools) are common symptoms of gastrointestinal disorders associated with diarrhoea or constipation. How is stool shaped in its final form? The question sounds trivial, but, besides reasoning on the basis of plausibility, we lack insights into the physiological mechanisms. In the present issue of *The Journal of Physiology*, Costa *et al.* (2021) provide answers by revealing the mechanism of pellet formation in guinea-pigs. In this species, the proximal colon is filled with an unshaped faecal mass, whereas well-formed pellets appear in the distal colon. The formation of discrete pellets happens at the transition between the proximal and distal colon, in the so-called colonic flexure, although the forces behind this transformation are unknown. The study by Costa *et al.* (2021) shows that the water content of the luminal material decreases continuously along the colon until the rectum, with no abrupt change at the colonic flexure. Therefore, the appearance of formed pellets is probably not explained by sudden changes in viscosity. After determining the physiological flow rates inside the colon, they infused artificial contents of different consistency in isolated large bowel preparations, and then electromyographic activity was detected and movements were followed by video imaging.

In the experiments of Costa *et al.* (2021), the isolated large intestine readily forms pellets, demonstrating that this procedure requires neither a connection to the central nervous system, nor the influence of blood-borne factors. They describe proximal colonic migrating motor complexes (PCMMPs) that move the content as they propagate from the oral end of the colon towards the flexure. Here, a small piece is pinched off creating a pellet-like bolus, which is forwarded at a higher speed along the distal colon. Damage to the neural elements and muscle at the colonic flexure with or without the proximal colon, but not to the proximal colon alone, abolishes pellet formation. What makes the colonic flexure so special? Costa *et al.* (2021) managed to decipher a new myogenic mechanism localized to the flexure, namely slow phasic contractions propagating a few centimetres in both oral and aboral directions. Interestingly, these occur at $\sim 3\times$ higher frequency than the PCMMPs in the proximal colon, creating opposing anterograde and retrograde forces around the flexure, which probably contribute to shaping of the faecal material into pellets. An intriguing speculation by Costa *et al.* (2021) is that, based on a similar cyclic myogenic pattern in the human sigmoid colon (Dinning *et al.* 2014), the sigmoid-rectal junction in humans might be the equivalent of the guinea-pig colonic flexure.

With their study, Costa *et al.* (2021) focused on motor patterns. This is reasonable, particularly because mere changes in viscosity have no influence on gastric or intestinal motility as measured by contractile amplitude and frequency, motility index or propagation length of intestinal contractions (Ehrlein *et al.* 1987). Therefore, the immediate notion that absorption will thicken the faeces and thereby influence wall movements does not apply. Nevertheless, it remains to be explored how a co-ordinated action between motility, secretion and absorption are involved in the process of pellet formation. Clearly, there must be a role for water and ion movements across the mucosa to support the transition from watery content to formed stool. In addition, it is important to investigate the role of different foods in stool formation with the aim of understanding which nutritional strategies may help form a normal stool.

One other factor shaping the stool could be the elastic property of the gut wall. Wombats (furry Australian marsupials) are unique in that their droppings have a cubic shape. By analysing the content in different sections of wombat intestines, Yang *et al.* (2021) found that the final form is obtained before reaching the terminal colon. They concluded that the cubic shape is created by non-uniform thickness and stiffness of the colonic wall in combination with a reduction in water content and peristaltic movements. Although Yang *et al.* (2021) did not analyse stiffness differences between sections of the gut, the question emerges of whether a different elastic property at the colonic flexure may contribute to pellet formation in the guinea-pig.

The presence of formed pellets in the distal colon is for another reason relevant. Recently, Kamphuis *at al.* (2017) challenged the widely accepted view of a colonic mucus layer covering the epithelium of the entire colon, protecting the mucosa from the luminal content. They observed that, in the proximal colon, the secreted mucus was mixed into the chyme, enabling the bacteria and digesta to get in contact with the mucosa. However, around the colonic flexure, where firm pellets started to appear, they were evenly covered with a mucus layer, therefore isolating the bacteria inside the pellets from the colonic wall. This finding suggests that the appearance of a separating mucus layer requires the presence of a firm pellet. Therefore, we can assume that a disturbance in pellet formation probably leads to a non-physiological direct contact of faecal bacteria with the mucosa of distal colon, with possible deleterious effects to the host.

Explorations of the mechanisms leading to stool formation in humans should help our understanding and management of long-term functional complications, such as diarrhoea or faecal urgency, after colorectal surgeries involving the sigmoid-rectal junction (Annicchiarico *et al.* 2021). The study by Costa *et al.* (2021) marks an important milestone along this way.

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Additional information

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