

# Hydrogen Sulfide in Rumen

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Hydrogen sulfide is a Janus-faced molecule with many beneficial and toxic effects on the animal health. In ruminants, rumen fermentation plays a vital role in the digestion and absorption of nutrients. During rumen fermentation, the production of hydrogen sulfide can occur, and it can be rapidly absorbed into the body of the animals through the intestinal wall. If the production of hydrogen sulfide concentration is higher in the rumen, it can cause a toxic effect on ruminants known as poliomyelitis. The production of hydrogen sulfide depends on the population of sulfate-reducing bacteria in the rumen. In rodents, H<sub>2</sub>S maintains the normal physiology of the gastrointestinal tract and also improves the healing of the chronic gastric ulcer. In the gut, H<sub>2</sub>S regulates physiological functions such as inflammation, ischemia–reperfusion injury and motility. In this review article, we summarize the toxicity occurrence in the body of animals due to high levels of hydrogen sulfide production and also recent progress in the studies of physiological function of H<sub>2</sub>S in the gut, with a special emphasis on bacteria-derived H<sub>2</sub>S is discussed in this review.

Keywords: rumen ; hydrogen sulfide ; ruminants ; fermentation ; animal health

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## 1. Introduction

The crucial life-supporting role of hydrogen sulfide (H<sub>2</sub>S) has developed from microorganisms to plants, invertebrate, vertebrate, and, lastly, to mammals [1]. H<sub>2</sub>S has only been known as a poisonous gas and ecological hazard. Earlier studies have shown that in animals, H<sub>2</sub>S is the most poisonous gaseous signaling molecule, after nitric oxide and carbon monoxide [2]. Recently, H<sub>2</sub>S was recognized as the third most physiologically significant gasotransmitter and plays a crucial role in various cell signaling pathways. H<sub>2</sub>S is an endogenous signaling molecule that may establish using protein sulfhydration to control different physiological functions. Hydrogen sulfide is also a byproduct of dietary sulfate metabolism by gut bacteria [3]. An increasing number of research studies have established hydrogen sulfide gas as an important cytoprotectant and redox modulator. In addition, H<sub>2</sub>S has a pleiotropic impact on the physiology of animals [3]. Consequently, a more important function of hydrogen sulfide was recognized as protecting from oxidative stress and ischemia–reperfusion injury by various mechanisms, for example, maintaining the level of glutathione (GSH) and directly suppressing mitochondrial reactive oxygen species (ROS) [4]. H<sub>2</sub>S also inhibits cytotoxic CD8+ T cells, though this happens at what we currently consider to be a supraphysiological level of hydrogen sulfide [2]. Production of hydrogen sulfide in mammalian tissue has been known for a long time, but it was primarily ignored as metabolic waste. A significant level of hydrogen sulfide has been detected in mammalian tissue from human, cow and rat in the range of 50–160  $\mu\text{M}$  [1]. Emerging studies have shown that H<sub>2</sub>S can serve as a potential barrier against antibiotics and oxidative stress [3][5]. In addition, hydrogen sulfide has been found to regulate several antioxidant enzymes such as ascorbate peroxidase (APX), catalase (CAT), super oxidase dismutase (SOD) and glutathione reductase (GR) [6]. H<sub>2</sub>S also plays a vital role as an intracellular gaseous transmitter in various physiological and pathologic mechanisms in rodents [7]. In addition, H<sub>2</sub>S plays a crucial role in the physiological function and maintenance of the gastrointestinal tract. In the rat colon, it regulates the secretion of calcium ion through activating the Ca<sup>2+</sup> and ATP sensitive K<sup>+</sup> [8]. In addition, rats treated with H<sub>2</sub>S improved the healing of a chronic gastric ulcer [9][10].

In any case, the natural and physiological significance of this chemical in endogenous hydrogen sulfide digestion has not been completely determined. Hydrogen sulfide is oxidized successively in the mitochondrion to thiosulfate and afterwards to sulfite, with the end result under physiological conditions being sulfate [11].

Hydrogen sulfide and its different ionic forms are highly toxic forms of sulfur. In the rumen, microbes produce sulfide—and if the diet contains more sulfate—the microbes produce a greater quantity of sulfide. In the rumen, dietary sulfur can be compressed into hydrogen sulfide. Hydrogen sulfide is a type of gas and its accumulation in ruminants may create some kind of toxic effects on the animals. It may cause some disorders, such as poliomyelitis [12]. In ruminants, poliomyelitis causes neuropathological conditions, leading to neural metabolic disorders, as, change in the level of thiamine, water deprivation, sodium ion toxicosis, higher intake of the sulfur and lead poisoning [13]. Hence it is important to regulate the production of hydrogen sulfide in the rumen.

## 2. Hydrogen Sulfide Toxicity in Rumen

Hydrogen sulfide's effects on respiration are similar to that of hydrogen cyanide <sup>[14]</sup>. Hydrogen sulfide and its ionic particles are extremely lethal and have a strong effect on animals. Rumen fermentation produces hydrogen sulfide, which is quickly absorbed through the intestinal wall and making animal sensitive to the toxin hydrogen sulfide. The production of hydrogen sulfide depends on the sulfur concentration in the diet <sup>[15]</sup>. If the sulfur is provided to animals in the form of sulfate—or the concentration of sulfur in the diet is greater—the microorganisms in rumen use the sulfate to synthesize sulfides, which increases hydrogen sulfide levels in the rumen of the animals. This extreme absorption and production of sulfide in rumen causes a toxicological effect on the health of the ruminants <sup>[16]</sup>. Abe et al. (1996) <sup>[17]</sup> reported that hydrogen sulfide may act in the brain as a neuromodulator. Gould et al. (1997) <sup>[13]</sup> also stated that usually, when the concentration of hydrogen sulfide exceeded 2000 mg/L it may cause the poliomyelitis, and death may occur if animals are not cured timely. Many studies also reported that greater production of hydrogen sulfide levels could cause sulfur-induced poliomyelitis (S-PEM) in animals. Lewis et al. (1954) <sup>[18]</sup> reported that hydrogen sulfide concentration below 471.2 mg/L in rumen did not cause toxic and side effects on the health of animals.

## 3. Hydrogen Sulfide Production Pathway in Rumen

### 3.1. Hydrogen Sulfide Production in Rumen

The production of  $H_2S$  in the rumen is depending on the availability of sulfate reduction by ruminal sulfate-reducing bacteria. In the rumen, so many bacteria, fungi and protozoa are present, some bacteria are sulfate-reducing bacteria (SRB) and these bacteria are anaerobic. These bacteria can reduce sulfate into hydrogen sulfide in the rumen of the animals <sup>[19]</sup>, and the reaction is demonstrated in Figure 1. Lewis et al. (1954) <sup>[18]</sup> verified that in the rumen of sheep, sulfate could be reduced into hydrogen sulfide. It was also confirmed in the in vitro trial that substance-reducing particles in fermentation broth could be reduced by the use of numerous sources, for example, ethanol, glucose, malic acid, citric acid and lactic acid. Though in 1960, the first strain of SRB was isolated, research on sulfate reduction in the rumen was conducted during the 1953. *Desulfovibrio* is SRB major strain that was found in the rumen by Howard et al. <sup>[20]</sup>. Cummings et al. (1995) <sup>[21]</sup> conducted research on steers fed high sulfate diet and concluded that there was no upsurge of SRB population, but the capability to decrease sulfate in the rumen was boosted. The source of sulfur (S) performs a vital role in the use of S and the concentration of  $H_2S$  in the rumen of ruminants—especially in an increased dietary S in total mixed ration. Availability of S for ruminal reduction is more useful than total S in the diet since the differences in ruminal  $H_2S$  concentration is successfully evaluated in ruminal protein sulfur and ruminal S availability (RAS) intakes instead of total intake of S <sup>[22]</sup>. Following an in vitro technique, the individual ingredients can be used to predict the coefficient of RAS. Meanwhile, the intake form can be controlled by the concentration of  $H_2S$  in the ruminants. The organic source of S is methionine and can be absorbed easily as amino acids. This makes it unavailable for the reduction in the rumen to sulfide and the reverse is true; thus, the inorganic source of S is vulnerable to be metabolized in the rumen to form other dangerous compounds, including  $H_2S$ . Therefore, the concept of RAS is vital to predict  $H_2S$  concentration in the rumen instead of focusing the available S in the diet <sup>[23]</sup>.

**Figure 1.** Sulfur-reducing bacteria use the sulfate to produce hydrogen sulfide.

### 3.2. Sulfide-Reducing Bacteria and Methanogens Relationship in the Rumen

There is an interactive and competitive relationship among methanogens and SRB. SRB and methanogens compete with each other for the requirement of the hydrogen for metabolism through anaerobic reactors <sup>[24]</sup>. Correspondingly, in the rumen, as SRB reduce sulfate to sulfide and methanogens reduces  $CO_2$  to produce  $CH_4$ . SRB can also competitively attach to hydrogen ions. In the rumen, SRB's compatibility with methanogens depends mainly on the sulfate levels <sup>[25][26]</sup>. If sulfate levels exceed a certain concentration in the rumen, the production of methane can be decreased. Nevertheless, when the concentration of sulfate becomes very low, a mutually beneficial and symbiotic association develops through hydrogen generation among methanogens and SRB, signifying 'interspecific transfer of hydrogen. Reducing the level of sulfates in the rumen by SRB can make SRB a source of hydrogen sink <sup>[27]</sup>. Taking into account the two considerations of thermodynamics and matrix affinity, SRB has an advantage in competing with methanogens for hydrogen <sup>[28]</sup>. However, few studies have shown that methanogens cannot contest with SRB for hydrogen, though SRB and methanogens coexist <sup>[29][30]</sup>. The absolute benefit of SRB in the use of hydrogen is similarly verified by the kinetic parameters of the potential difference. The hydrogen ion is more inclined towards SRB, since the energy provided by the sulfates is greater. SRB has a low value of usable critical level for hydrogen relative to methanogens. Hence, the lower level can be used by SRB as opposed to that of methanogens. Furthermore, the temperature is also a significant aspect of the rivalry among methanogens and SRB for hydrogen. SRB dominates under moderate temperature circumstances (37 °C); however,

methanogens have significant advantages in high-temperature settings (55 °C) [31]. Erin et al. (2011) reported that the level of H<sub>2</sub>S in rumen of same diet cattle were change due to the change in the SRB population in the rumen of each cattle[32].

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