



Metropolia

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Characteristics of breathing patterns and neurological control mechanisms of Equine and Canine diaphragm during tidal breathing: a scoping review

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Abstract

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The purpose of this study was to form a synthesis about neurological control mechanisms of equine and canine diaphragm and the species-related characteristics of their breathing patterns during tidal breathing.

Furthermore, this study aimed to provide profound insight behind osteopathic rationale in relation to neurological control mechanisms of equine and canine diaphragm and species-related characteristics of their breathing patterns during tidal breathing for osteopaths treating equine and canine patients.

This study was conducted as a scoping review. Searches were carried out in ProQuest Central, Science Direct and Wiley Online Library databases in March 2025. Peer-reviewed complete studies and reviews in English related to breathing pattern and neural control mechanisms of canine and equine diaphragm during tidal breathing were included. Moreover, an additional hand-search from journals and reference lists of chosen articles was done. Data searches were conducted without date restriction. Non-peer reviewed data such as book chapters, theses, dissertations and websites were excluded from the data sources.

Altogether the database searches provided 348 results from which 8 articles remained to be included into the analysis after title, abstract and full text screening. Moreover, additional 8 manually searched articles were included to the analysis phase. Thus, finally 16 articles were analysed by using thematic analysis. The following six main themes were constructed based on the selected articles: 1) Metabolism is the primary motor for gas exchange; 2) Physical properties of respiratory system in both equine and canine species; 3) Parts of tidal breathing pattern; 4) The respiratory control during tidal breathing; 5) Individualized blueprint for optimal breathing pattern and 6) Differences in species-related mechanical properties of respiratory system.

The results of this study suggest that wider recognition of the characteristics of healthy, normal tidal breathing patterns and multilayered neural control of the diaphragm in equines and canines would be beneficial for animal osteopaths and for their patients.

Keywords: osteopathy, animal osteopathy, equine osteopathy, canine osteopathy, tidal breathing pattern, diaphragm, respiratory neural control

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Tämän ylempään ammattikorkeakoulun opinnäytetyön tarkoitus oli muodostaa synteesi hevosen ja koiran levon aikaisten hengitysmallien lajityypillisistä ominaisuuksista sekä pallean hermotuksellisesta säätelystä.

Opinnäytetyön tavoitteena oli käsitellä hevosen ja koiran levon aikaisten hengitysmallien lajityypillisiä ominaisuuksia sekä pallean hermotuksellisia säätelymekanismeja osteopaattisesta näkökulmasta ja siten tuottaa lisätietoa kyseisistä ilmiöistä osteopaateille, jotka hoitavat työssään hevos- ja koirapotilaita.

Opinnäytetyö toteutettiin kartoittavana katsauksena. Tiedonhauk suoritettiin ProQuest Central-, Science Direct- ja Wiley Online Library- tietokannoissa maaliskuussa 2025. Englanninkieliset, vertaisarvioidut, valmiit tutkimukset ja katsaukset liittyen hevosen ja koiran levon aikaiseen hengitysmalliin sekä pallean hermotukselliseen säätelyyn sisällytettiin tiedonhakuun. Lisäksi manuaalinen täydentävä tiedonhaku suoritettiin julkaisuihin ja valittujen tutkimusten lähdeluetteloihin pohjautuen. Tiedonhauk suoritettiin ilman aikarajaa. Ei-vertaisarvioidut lähteet, kuten kirjanluvut, opinnäytetyöt, internet-lähteet ja väitöskirjat rajattiin pois tiedonlähteistä.

Kokonaisuudessaan tiedonhaku tuotti 348 tulosta, joista 8 artikkelia jäi sisällytettäväksi sisällönanalyysiin otsikko-, abstrakti- ja kokotekstiarvioinnin jälkeen. Lisäksi 8 manuaalisesti haettua artikkelia valittiin mukaan sisällönanalyysiin. Siten yhteensä 16 artikkelia valittiin lopulliseen temaattiseen analyysiin. Seuraavat kuusi pääteemaa muodostettiin luotiin pohjautuen valittuihin artikkeleihin: 1) Aineenvaihdunta on tärkein vaikuttaja elimistön kaasujenvaihdon taustalla; 2) Hevosen ja koiran hengityselimistön fyysiset ominaisuudet; 3) Lepo hengitysmallin osat; 4) Hengityksen hermotuksellinen säätely lepo hengityksen aikana; 5) Optimaalisen lepo hengitysmallin yksilöllinen kaava ja 6) Hengityselimistön fyysisten ominaispiirteiden lajien väliset erot.

Opinnäytetyön tulosten perusteella laajempi ymmärrys hevosen ja koiran terveiden, normaalien lepo hengitysmallien ominaisuuksista sekä pallean moniulotteisesta hermotuksellisesta säätelystä olisi hyödyksi eläimiä hoitaville osteopaateille sekä heidän potilailleen.

Avainsanat: osteopatia, eläinosteopatia, hevososteopatia, koiraosteopatia, lepo hengitysmalli, pallea, hengityksen hermotuksellinen säätely

Tämän opinnäytetyön alkuperä on tarkastettu Turnitin Originality Check -ohjelmalla.

Contents

1	Introduction	1
2	Theoretical background	3
2.1	Respiratory muscles	3
2.2	Morphogenesis and configuration of mammalian diaphragm	4
2.3	Breathing pattern	6
2.4	Tidal breathing	6
2.5	Neurological control during tidal breathing	7
2.6	Diaphragm in osteopathy	9
2.7	Osteopathy	9
2.8	Animal osteopathy	11
2.9	Animal welfare in osteopathic care	12
3	Purpose and aim	14
4	Methodology	15
4.1	Scoping review as a method	15
4.2	Review protocol	16
4.2.1	Search strategy and eligibility criteria	17
4.2.2	Study selection and critical appraisal	19
4.2.3	Data extraction and synthesis	22
4.2.4	The process of code generation	23
4.2.5	Theme construction	24
4.3	Scoping review quality assessment	25
5	Results	27
5.1	The general characteristics of the equine and canine breathing patterns	29
5.1.1	Metabolism is the primary motor for gas exchange	29
5.1.2	Physical properties of the respiratory system in both equine and canine species	31
5.1.3	Parts of tidal breathing pattern	34
5.2	The neurological control mechanisms of the equine and canine diaphragm during tidal breathing	37
5.2.1	The respiratory control during tidal breathing	37
5.3	The species-related differences of equine and canine breathing patterns during tidal breathing	42
5.3.1	Individualized blueprint for the optimal tidal breathing pattern	42

5.3.2	Differences in species-related physical properties of the respiratory system	44
6	Discussion	48
6.1	Summary of the findings	48
6.1.1	Metabolism as the main drive for the ventilation	48
6.1.2	Physical properties of the respiratory system set the circumstances for breathing	49
6.1.3	Typical parts of tidal breathing	49
6.1.4	The neural control of the tidal breathing	49
6.1.5	Tidal breathing patterns of equine and canine species	51
6.1.6	Species-related differences in the physical properties of the respiratory system	51
6.2	Interpretations, possible explanations and potential implications	52
6.3	Limitations, ethical considerations and validity of scoping review	57
6.4	Future recommendations	59
7	Conclusions	60
	References	61
	Appendices	
	Appendix 1. Data search strategy	
	Appendix 2. The summary of data from selected articles including the quality assessment	
	Appendix 3. The initial codes of the thematic analysis	

1 Introduction

Breathing is essential for life in all mammals. Life of them depends on continuous input of energy to fulfil requirements of very basic function of organism, the metabolic processes. Primarily, these processes withdraw energy from the environment and make it available for organism to sustain life. Metabolic processes include continuous manufacture, maintenance and selective destruction of complex structures of living cells, which demands uninterrupted energy supply. Maintenance of cellular homeostasis is necessary for optimal metabolism and vice versa. For the metabolic needs to be filled, sufficient gas exchange is essential, which in mammals is achieved by pulmonary respiration. (Wilson & Matschinsky 2021:1,2.)

Taking a breath requires involvement from numerous structures of the body, from which diaphragm has a significant role. Thus, initiation of the breathing pattern and establishment of the tidal volume is a complex process requiring synchronous neural communication. (Braun 1990: 226). In addition, during evolution, precursor of diaphragm appears to be very ancient structure in animals. Merrel & Kardon (2013: 4027) highlight that some variant of septum separating lungs from abdominal viscera exists already in birds and reptiles but diaphragm as a muscularized structure is unique to mammals. Consequently, chosen breathing pattern varies between the mammalian species corresponding to their anatomical characteristics and metabolic requirements.

Furthermore, the diaphragm has been considered as one of the key elements in osteopathic treatment since the early history of osteopathy. According to the founder of osteopathy, Still (1899:123) the diaphragm, when not in normal position and its supporting structures not all in line, is perhaps the least understood as the cause of great quantity of diseases. As Patterson (2006:593) suggests, within osteopathic profession there is a great need for deeper understanding of underlying biology behind the mechanisms of osteopathic manual treatment which could be achieved by using animal models to better evaluate the osteopathic principles in actual function.

Both canine and equine species (with the absence of excessive selective breeding) have very high capacity of pulmonary gas exchange as measured by lung diffusing capacity. Among other mammals, horse and dog have extraordinary superior O₂ transport system (e.g. in comparison to best human athletes) resulting in great athletic capacity

of these species. During their evolution function of diaphragm as a stabilizer and visceral organizer may have had a great role in allowing the simultaneous respiration and locomotion. The diaphragm of a horse comprises almost 1% of the total body mass, is highly vascularized and contains a rich network of mitochondria resulting in high oxidative capacity of this muscle. (Perry, Similowski, Klein & Codd (2010:12; Poole & Erickson: 2011:9,29.) For an osteopath to recognize any alterations, it is essential to first understand diaphragm's normal function in health and to be able to identify the characteristics of normal breathing pattern.

The purpose of the current master thesis is to form a synthesis about the neurological control mechanisms of the equine and canine diaphragm and the species-related characteristics of breathing patterns during tidal breathing. Consequently, better understanding of the control mechanisms of diaphragm and recognition of the species-specific breathing patterns improves accuracy and safety of osteopathic treatment offered to equine and canine patients. Furthermore, this work aims to provide additional information about physiological rationale behind osteopathic approach for animals to other professionals, such as veterinarians, animal physiotherapists and animal trainers, but also for caretakers of animals who seek relief for their animal companions.

2 Theoretical background

2.1 Respiratory muscles

Synchronized neural activation of several skeletal muscles creates a negative intrathoracic pressure to suck air into the lungs. This phenomenon is called as the inspiratory pump. A transdiaphragmatic pressure driving air into lungs is created mainly by diaphragm and its neural activation. Therefore, diaphragm is considered one of the key elements for inspiration. (Fogarty, Mantilla & Sieck 2018:113.) Among diaphragm, also internal intercostals can be included into the muscles of the inspiratory pump. (Del Negro, Funk & Feldman 2018: 353). During the contraction of diaphragm intra-abdominal pressure increases, and intrathoracic pressure decreases. (Fogarty et al 2018:116)

During tidal breathing accessory muscles of inspiration and muscles of expiration remain mostly passive in healthy humans. Interestingly, same is not the case with equine species at rest, since the healthy horses embrace the biphasic breathing pattern with active and passive components both during inspiration and expiration. (Moreno-Martinez, Byrne, Rasis, Waldmann, Hosgood & Mosing 2022:1). Whereas in dogs, the typical breathing pattern resembles more that of the humans and the expiratory phase is usually mostly passive.

Muscles of respiration can be divided into two groups: inspiratory and expiratory muscles. Diaphragm, external intercostals, parasternal, scalene and sternocleidomastoid muscles form the group of inspiratory muscles, whereas internal intercostals, transverse abdominis, external and internal oblique and rectus abdominis form the group of expiratory muscles. (Ratnovsky, Elad & Halpern 2008: 82.) Additionally, the muscles of upper airways do not only participate in orofacial behaviours such as swallowing, coughing, phonation and sneezing, but also act as accessory respiratory muscles. Genioglossus, geniohyoid and tensor and levator veli palatini muscles maintain the upper airways unobstructed during breathing even though they do not directly move air in and out of the lungs. (Kubin 2016:3.) Horse is an obligatory nasal breather and therefore the muscles of their upper airways are of a key importance in maintaining the upper airways adequately open during breathing. (Cook 1981; Mellor & Beausoleil 2017:3).

2.2 Morphogenesis and configuration of mammalian diaphragm

Diaphragm is one of the defining structures of mammals among the body hair and mammary glands. (Perry et al 2010:1). Diaphragm is a dome-shaped internal skeletal muscle located inside thorax forming a physical barrier between thorax and abdominal cavity. The orientation of diaphragm is oblique within the thoracic cavity, where the dorsal margin extends further caudally than the ventral one ending to the xiphoid process of the sternum. In healthy individuals the diaphragm separates paired pleural cavities completely from the abdomen. Diaphragm has traditionally considered to be mainly related to respiration function but also acts as a gastrointestinal barrier. (Kocjan et al 2017:225; Perry et al 2010:5; Pickering & Jones 2002: 308,305.)

Diaphragm is a peculiar characteristic for mammals which allowed them to evolve as performant warm-blooded animals capable of collateral respiration and movement. (Merrell & Kardon 2013: 4027). The evolutionary development of diaphragm may be related to the less compliant mammalian lung tissue structure, in comparison to reptiles, caused by the gradual evolution of the alveolar structure. (Perry et al 2010:12).

Instead of only focusing the respiration function, there is growing evidence about the importance of diaphragm in other bodily functions, such as acting as a gastrointestinal barrier. (Pickering & Jones 2002:305). Kolar, Neuwirth, Sanda, Suchanek, Svata, Volejnik, & Pivec (2009:391) suggest that there is a synchronization between the respiratory movement of diaphragm and its stabilization capacity of the body. According to Kolar (2006: 532) there is a correlation between the diaphragm contraction and stabilization of the spine and torso which enables correct activation of the muscles inserting on the upper and lower extremities. Evans & de Lahunta (2013 :224) and Merrell & Kardon (2013:4027) describe that the changes in muscular activity of the diaphragm are related to swallowing and vomiting but also to stabilization of the position of abdominal viscera during locomotion.

There are several structures which traverse the diaphragm: the vena cava, the esophagus and the aorta, from which the last two pass through the crural part of the diaphragm. (Pickering & Jones 2002: 308; Perry et al 2010:6) The shape of central tendon varies between different species of mammals. The vena cava perforates through the central tendon from its right side. (Perry et al 2010:5.) According to Bordoni & Zanier (2013:282) the great and minor splanchnic, radix medialis of azygos vein and radix medialis of hemiazygos vein also cross the diaphragm between its pillars, which attach to

the ventral aspect of the lumbar spine at the level of L2 to L4. According to Bellissimo and Goligher (2024:665) the diaphragm is characterized by dense vascularization receiving its arterial supply from the right and left inferior phrenic arteries, the musculophrenic branches of internal mammary arteries, the intercostal arteries and minor supply from pericardiophrenic arteries, whereas the venous drainage is carried out by the inferior phrenic veins.

Morphogenesis of completely functioning diaphragm is crucial for mammalian respiration and for correct organization of the internal visceral organs. Multiple embryonic derivatives form the complete, adult diaphragm. (Sefton, Gallardo & Kardon 2018: 64.) Embryologically, the diaphragm and its associated connective tissue is formed from four parts: the septum transversum, dorsal mesentery of the esophagus, the pleuroperitoneal folds and the sidewalls of the body. (Merrell & Kardon 2013: 4027; Lessa, de Abreu, Bertassoli & Ambrósio 2016: 123). According to Merrell & Kardon (2013:4027) the septum transversum is the first present structure during the development of diaphragm and has a similar configuration, thin sheet of mesodermal connective tissue, in all vertebrates. Pleuroperitoneal folds are the second important component during the development of the diaphragm which are described as two pyramidal-shaped structures on each side of the esophagus originating from the body wall between pleural and peritoneal cavities. (Merrell & Kardon 2013: 4028). Dorsal mesentery of the esophagus contributes into the development of the crural part of the diaphragm which forms the pillars or crus attaching to the lumbar vertebrae. (Lessa et al 2016: 123).

Finally, as fully formed anatomical structure diaphragm can be divided into costal and crural diaphragm which join at the region of central tendon at apex of domed diaphragm. Central tendon attaches to liver via the falciform and coronary ligaments. As mentioned above, developmentally the diaphragm consists of several adjacent origins, which may explain the differences in the function of costal and crural parts. Costal part of the diaphragm is more related to breathing and barrier function between the thoracic and abdominal cavity, whereas the crural part attached to the vertebrae and surrounding the esophagus is more related to swallowing function. (Sefton, Gallardo & Kardon 2018:64; Pickering & Jones 2002:306 & Merrell & Kardon 2013:4027.) During swallowing and esophageal distension, the crural and costal parts of the diaphragm differ in activity to allow a food bolus to transit across the diaphragm without interrupting the respiration. (Pickering & Jones 2002: 306).

According to Kozłowska, Wierzbicka, Jasiński & Domino (2022: 381) horse as a prey animal has a significant functional plasticity of the respiratory system, which has enabled the fast escape from predators during the evolution of this species. Understanding of the interspecies differences in breathing strategies is crucial to osteopaths who treat animals. According to Haltmayer, Reiser, Schramel & van den Hoven (2013:658) the breathing strategy of horses differs from standing humans.

2.3 Breathing pattern

Sufficient gas exchange in mammals results from adequate pulmonary ventilation which is the result of optimal breathing frequency, and the amount of air inhaled during each breath. (Howell 2006: 18). Pulmonary and alveolar ventilation are directly proportional to the metabolic rate of an animal. (Mortola & Maskrey 2011). One of the primary homeostatic functions of the respiratory system is the regulation of blood gas composition which is consistent with the maintenance of cellular homeostasis. The blood gas and cellular level homeostasis is achieved with minimal respiratory work in respect of the mechanical properties of the respiratory system of the considered animal, resulting in adoption of certain breathing pattern in mammals of different sizes, and with different mechanical properties of their respiratory systems. (Gomes & Blenis 2015: 110; Clancy & McVicar 1996: 16.)

The rhythm of respiration is created by the respiratory central pattern generator (rCPG) in the brainstem. (Oku 2022:5). The adoption of optimal breathing pattern is not only more beneficial for better pulmonary function but also favours the cell homeostasis maintenance by supporting the proper gas exchange. Sikora, Mikołajczyk, Łakomy, Karpiński, Żebrowska, Kostorz-Nosal & Jastrzębski (2024:8) observed in their recent study that the adoption of the diaphragmatic breathing pattern had a significant effect on lung function in endurance-trained human athletes.

2.4 Tidal breathing

Normal respiration with relatively constant rate and inspiratory/expiratory volumes is defined as tidal breathing. The motor behind tidal breathing is a group of primary and accessory inspiration muscles from which the diaphragm is the most important. (Russo, Santarelli & O'Rourke 2017:300.) The evolutionary development of a rhythmic inspiratory activity is proposed to be significant in increasing the efficiency of costal breathing,

which is promoted by the expansion of the lower rib cage, by prevention of the aspiration of the abdominal content into thorax during inspiration and by caudal push of the abdominal mass away from the expanding lungs. (Perry et al 2010:12).

The frequency of breathing rhythm varies between individuals. (Lehrer & Gevirtz 2014: 1,2). During tidal breathing, the normal respiratory frequency of a horse is approximately 10-15 breaths/min and tidal volume approximately 5-6 litres. (Mellor & Beausoleil 2017: 41). Whereas in dog the normal respiratory frequency is 18-25 breaths/min. (Englar 2019:1). The normal tidal volume of a dog is highly variable due to great variations in the size of different dog breeds, with a range of 10 to 20 ml/kg. (Donati, Tarragona, Araos, Zaccagnini, Díaz, Nigro, Sáñez, Plotnikow, Staffieri & Otero 2024: 408).

During the exhalation relaxation of the diaphragm occurs resulting in a comparative resting position, which is influenced by the balance of forces between the lung and the thoracic body wall. (Lessa, de Abreu, Bertassoli & Ambrósio 2016: 125). The apex of the diaphragm and junction between the diaphragmatic and costal pleura move in synchrony during tidal breathing. The lung volume and the diaphragm range of motion are remarkably correlated during tidal respiration. (Kolar 2009:391.)

According to Kolar's findings (2009: 388) the tidal breathing frequency and volume varies between individuals, but no correlation between the diaphragmatic range of movement and the body weight, body mass index (BMI) or height of the participants was found during tidal breathing. Kocjan, Gzik-Zroska, Nowakowska, Burkacki, Suchon, Michnik, Czyzewski & Adamek (2018:6,8) found that the greater range of diaphragm movement during tidal breathing is related to better equilibrium parameters via relationship between the neural activity of the vestibular and the autonomic nervous system.

2.5 Neurological control during tidal breathing

Well-functioning respiratory system requires coordination of various neural structures at central and peripheral level. Breathing is a complex phenomenon which is controlled both by autonomously via the brainstem and voluntarily by activity of the motor cortex. During the autonomous or reflex control of breathing, the strength, timing and frequency of respiratory muscle contractions are influenced by the combined activity of several nuclei in the medulla stimulating pools of inspiratory motor neurons. The normal spontaneous pattern of breathing (tidal breathing) is generated by the activity of these neurons which is affected by four major kinds of afferent, i.e. sensory, inputs including: 1) sensory input from central and peripheral chemoreceptors reacting to

changes (e.g. PO_2 , PCO_2 , pH) in arterial blood and cerebrospinal fluid; 2) sensory feedback from several structures of respiratory system (e.g. airways, lungs, respiratory muscles and chest wall); 3) afferent input from the muscles of locomotion and 4) afferent information from several higher brain centres. Instead, the voluntary control of breathing involves the motor commands from the primary motor cortex which enables respiratory control during exercise, breath-holding and vocalization by interrupting the regular breathing rhythm. (Mellor & Beausoleil 2017: 41.) The diaphragmatic inspiration is driven by phrenic nerve activity steered by the central pattern generator in the brain stem. (Elstad, O'Callaghan, Smith, Ben-Tal & Ramchandra 2018:H7).

Merrell & Kardon (2013:4029) highlight that not only the synchronized morphogenesis of muscle, connective tissue and tendon structures during the embryologic development is required, but also proper vascular and neural development, to produce a fully functional diaphragm. According to Hudson, Gandevia & Butler (2017: 7082) during tidal breathing, the inspiratory muscles function in co-ordination, but with variety of activation patterns.

According to Fogarty et al (2018:117, 119, 120) the muscle activation of the diaphragm includes five major components: 1) phrenic motor neurons; 2) central pattern generators in the brainstem and spinal cord in charge of timing and arrangement of the rhythmic motor behavior; 3) pre-motor neurons located in the ventrolateral medulla which transmit the signals of the central pattern generator; 4) interneurons regulating pre-motor and/or phrenic neuron excitability and integrating the sensory feedback from receptors located in tissues related to breathing (e.g., afferent input from chemoreceptors, lung stretch or propriospinal feedback); 5) direct corticospinal connections to phrenic neurons allowing the voluntary control of breathing during different behaviors such as vocalization.

The diaphragm of a horse and dog is motorically innervated by the phrenic nerve originating from the spinal segments C5 to C7. (Ogawa 1959:745). The whole brachial and cervical plexuses are involved in the pathway of the phrenic nerve including an anastomosis with the vagus nerve, which joins to the medial longitudinal fasciculus and has a connection to the spinal trigeminal nucleus via sensory pathways. (Bordoni & Zanier 2013:288; Kocjan et al 2017:224). The left and right phrenic nerves supply motor innervation to each corresponding half of the diaphragm. The phrenic nerve includes sensory fibers as well which conduct the sensory innervation from the mid part of the diaphragm, but also from the adjacent pleura and peritoneum. (Kojcan 2017: 226.) The

general anatomy of the phrenic nerve innervating the diaphragm has been studied extensively but the knowledge about the anatomy and variations of distal rami of the phrenic nerves remains limited. (da Costa Pereira, Marsicano, Sanches, de Campos & Guedes 2022: 101). According to Alonso, Graham, Rustagi, Drazin, Loukas, Oskouian, Chapman & Tubbs (2017:672) also the subcostal nerve gives a small contribution to the motor and sensory innervation of diaphragm.

2.6 Diaphragm in osteopathy

Since the early history of osteopathy, the diaphragm has been an anatomical structure of great interest due to its' direct or indirect interconnectedness with all the parts of the body. According to Derenne, Debru, Grassino & Whitelaw (1994: 2234) the recognition of the diaphragm as a well-defined anatomical structure has its origins in the earliest Greek writings. The founder of osteopathy, Andrew Taylor Still described the diaphragm as following at the end of 1800th century:

All parts of the body have direct or indirect connection with this great separating muscle. It assists in breathing, in all animals, when normal, and when prolapsed by the falling in and down of any of the five or six ribs by which it is supported in place, then we suffer from the effects of suspended normal arterial supply, and venous stagnation below diaphragm. (Still 1899:124.)

According to Kocjan et al. (2017) and Bordoni & Zanier (2013:288) the function of diaphragm is considered being multifactorial, it is not only considered having a crucial role in breathing but plays an important role in multiple physiological systems, such as lymphatic, cardiac and vascular systems, pelvic floor function, posture, cervical spine stability and thoracic outlet function, as well as in the function of floor of the mouth and trigeminal system.

2.7 Osteopathy

Osteopathic healthcare has its foundation on an appreciation of the body as an incorporated whole with the focus on person-centredness, where the patients are treated as individuals and as equal allies in the business of healing, prevention, diagnosis and treatment of injury and illness. (Osteopathic International Alliance (2020:5) and Coulter & Oldham (2016:114). The practice of osteopathy is described as an application of the osteopathic principles combined with medical and scientific knowledge which aims to improve and contribute all aspects of individual's health. (EN16686 Osteopathic healthcare provision 2015: 8).

According to European Standard on Osteopathic Healthcare Provision (EN16686 Osteopathic healthcare provision 2015:8), osteopathic principles can be described as following:

- The human being is a dynamic functional unit, whose state of health is influenced by the body, mind and spirit; if one part is changed in the system, the balance of the whole pattern will be affected
- The body possesses self-regulatory mechanisms and is naturally self-healing; the human being always tries to regain its own dynamic balance and establish homeostasis
- Structure and function are interrelated at all levels of the human being.

Within osteopathic healthcare large range of techniques are used, including manual modalities for assessment and diagnosis of variety of health conditions related to musculoskeletal structures, nervous, circulatory and/or visceral system interfering with the body's physiological functions. The most frequently used manual techniques include joint mobilization and manipulation and soft tissue manipulation, but also self-management, wellbeing and lifestyle advice and support may be included. (Osteopathic International Alliance (2020:5,7.)

In Finland there are around 530 practising osteopaths, and the title 'Osteopath' is protected by law. Since 1994 osteopathy has been officially considered as a Healthcare Profession and The National Supervisory Authority for Welfare and Health (Valvira) supervises the use of the title 'Osteopath' as an occupational title of healthcare professional. (Regulation of the Osteopathic Profession in Europe 2023: 20.)

World Health Organization (2010: 8) lists the comprehension of the mechanisms of action of manual interventions and biochemical, cellular and anatomical response to therapy as one of the essential competencies for osteopathic practice.

As Patterson (2006:593) suggests, within osteopathic profession there is a great need for deeper understanding of underlying biology behind the mechanisms of osteopathic manual treatment which could be achieved by using animal models to better evaluate the osteopathic principles in actual function. According to recent analysis the studies of animal osteopathy are very small in numbers (Domingues, Franco, Rodrigues, Stilwell & Magalhães-Sant'Ana (2022: 196) but Thelwall (2021:8737) suggest in their citation

analyses that there is considerable amount of research interest in acupuncture, homeopathy, chiropractic and osteopathy in the veterinary field in addition to traditional veterinary approach. Consequently, further contribution into research field of animal osteopathy is required to provide comprehension about efficacy and safety of osteopathic treatment as one of the complementary therapies for animals.

2.8 Animal osteopathy

According to Nevin, Colles & Tozzi (2020:4) and Pusey, Brooks & Jenks (2010:2) the osteopathic treatment of animals and birds was undertaken occasionally already at the nineteenth century by osteopaths who had been trained to treat human patients. The principles of osteopathy can be applied to the treatment of animals, but it is crucial to respect the anatomical and physiological differences between species.

At the beginning a few cases were reported where the animals were brought to the osteopathic treatment by the patients who had benefitted from osteopathy themselves, and some osteopaths began to relieve the suffering of their own animals by osteopathic approach (Nevin et al 2020: 4). Farmers at rural areas contacted osteopaths from their region to seek help for their farm animals including several different species. (Pusey et al 2010:2).

Only during the last few decades, the field of animal osteopathy has gained greater interest from both the owners seeking relieve for their animals but also professionals from other disciplines aiming to multidisciplinary rehabilitation approach. The number of institutions offering training in animal osteopathy is still very limited worldwide. According to Haussler, King, Peck and Adair (2021) long tradition of various approaches to equine rehabilitation by both professionals and non-experts exists, some of which lack the profound understanding of their mechanisms of action, principles of physical therapy or awareness of tissue healing properties. Regarding to treatment of non-human animals it is crucial to respect their different way of expressing pain and discomfort, consequently understanding of the behavioral cues is required to assess the condition of the animal adequately.

Still today the amount of literature and research papers about the osteopathic treatment of animals is very limited mostly due to lack of funding (Nevin et al 2020:6). The use of Non-Conventional Therapies (NCT) in veterinary practice have been increasing in the recent years but the common guidelines or regulation for the providers of these

therapies is still lacking in the most of countries. (Domingues et al 2022:196). The knowledge base of equine rehabilitation practices has developed remarkably in recent years but deeper understanding of the underlying mechanisms of action and suitable dosage of therapeutic exercises, manual therapy and physical modalities is still limited (Hausler et al 2021:143). Therefore, more understanding of the possible mechanisms of osteopathic treatment of animals as one of the NCT treatment approaches is urgently needed.

2.9 Animal welfare in osteopathic care

The high-quality care in animal osteopathy needs to follow national and international regulations and laws. As an animal osteopath the animal welfare must be a key feature of the clinical practice. According to Association of Animal Osteopaths' Code of Conduct a detailed knowledge of the animal's anatomy and physiology, including the innate characteristics of each species being treated, is required from an Animal Osteopathic Practitioner. (AAO, The Association of Animal Osteopaths, n.d.). Monteiro, Lascelles, Murrell, Robertson, Steagall & Wright (2022:184) refer the animal welfare as following:

The current state that an animal finds itself in considering its physical and mental states and its relationship with the physical and social environments. (2022 WSAVA guidelines for the recognition, assessment and treatment of pain).

In private practice the owner of an animal often visits the osteopath before taking their pet to a veterinary professional which makes the osteopath to carry even larger load of liability of the animal's health. The following is stated at the Finnish Animal Welfare Act:

The objective of the Animal Welfare Act is to protect animals from distress, pain and suffering in the best possible way. It also aims to promote the welfare and good treatment of animals. Inflicting undue pain and distress on animals is prohibited. In addition, maintaining the health of animals must be promoted when keeping animals and the physiological and behavioral needs of the animals must be considered. (Animal Welfare Act, the Council Regulation (EC) No 1/2005)

When taking the animal's health and welfare into account it is highly important that the treating osteopath can point out even the slightest behavioral, anatomical and functional changes. According to Oliva, Baumgartner, Farris, Riegner, Khatib, Jung, Coghil & Fadel (2023:1785) breathing rate is a significant factor related to inter-individual differences in pain perception and manual approach could be included into multimodal

approach treatment of pain. Consequently, understanding the anatomical and physiological properties of the diaphragm and the species-specific characteristics of breathing pattern of an animal could improve the quality of osteopathic treatment of animals.

3 Purpose and aim

The purpose of the current master thesis was to form a synthesis about the species-related characteristics of the breathing patterns and neurological control mechanisms of the equine and canine diaphragm during tidal breathing for the osteopaths who treat equine and canine patients.

The aim of the study was to provide profound insight behind the osteopathic rationale in relation to the neurological control mechanisms of the equine and canine diaphragm and species-related characteristics of their breathing patterns during tidal breathing not only for osteopaths treating equine and canine patients, and to professionals, such as veterinarians, animal physiotherapists and animal trainers, but also for the caretakers of animals who seek relief for their animal companions.

The research questions were established as following:

- 1) *What are the general characteristics of the equine and canine breathing patterns during tidal breathing?*
- 2) *How is the equine and canine diaphragm neurologically controlled during tidal breathing?*
- 3) *What are the essential species-related similarities and differences in the breathing patterns between equine and canine diaphragm during tidal breathing?*

4 Methodology

4.1 Scoping review as a method

The scoping review included in this master thesis was conducted in line with the Joanna Briggs Institute (JBI) methodology for scoping reviews. The scoping review was chosen as a method of this study because the topic is novel in the research field of animal osteopathy, and it is a valid method to gather unexplored data. According to Mak & Thomas (2022:566) and Munn, Peters, Stern, Tufanaru, McArthur & Aromataris (2018:2) a scoping review is an applicable method in identifying gaps and mapping the literature on uncharted topics and in identifying key characteristics or factors related to a certain concept. Typically, the aim of a scoping review is to recognize the quality and quantity of the data regarding certain topic. Peters, Godfrey, McInerney, Munn, Tricco & Khalil (2020: 423) highlight that scoping reviews aim to find out the type of evidence available from the topic including both qualitative and quantitative data.

Scoping review can provide important knowledge to both research and practice purposes when the review title and question are formulated carefully. According to Peters et al (2020: 420) scoping review is a preferred choice as a review type when the more specific questions for evidence syntheses need still to be clarified and addressed. Peters et al (2020: 421) highlight that the aim of the scoping review is to provide a map or an overview of the existing evidence of certain subject.

Table 1. The scoping review framework applied from JBI approach to the conduct of scoping reviews (2015,2017, 2020)

	Scoping review framework proposed by Peters et al (2015, 2017, 2020)
1.	Definition and orientation of the objective/s and question/s
2.	Development and alignment of the eligibility criteria with the objective/s and question/s
3.	Representing the planned procedure to evidence searching, selection, data extraction and presentation of the evidence

4.	Exploring the evidence
5.	Selecting the evidence
6.	Eliciting the evidence
7.	Analysis of the evidence
8.	Presentation of the results
9.	Outlining the evidence in relation to the purpose of the review, drawing conclusions and determining any implications of the findings

4.2 Review protocol

According to Peters et al (2020:426) development of a scoping review protocol includes describing the review objectives, the way of reporting the results and the methods of the conducting the review to provide the information about the whole process in a clear, transparent way. PCC (population, concept and context) framework is a recommended tool in constructing clear and relevant objectives and acceptability criteria for a scoping review. (Pollock et al 2023: 522). In this master thesis a scoping review was initially conducted based on the following research questions established using the PCC approach:

- 1) *How is the anatomical configuration and what are the anatomical relationships of the equine and canine diaphragm during tidal breathing?*
- 2) *How is the equine and canine diaphragm neurologically controlled during tidal breathing?*
- 3) *What are the essential similarities and differences in anatomical configuration, anatomical relationships and neurological control mechanisms between equine and canine diaphragm during tidal breathing?*

However, after performing the initial search based on the stated research questions it became clear that there wasn't enough relevant data available to answer the first research question. Consequently, the research questions were refined as following:

- 1) *What are the general characteristics of the equine and canine breathing patterns during tidal breathing?*
- 2) *How is the equine and canine diaphragm neurologically controlled during tidal breathing?*
- 3) *What are the essential species-related similarities and differences in the breathing patterns and neurological control mechanisms between equine and canine diaphragm during tidal breathing?*

Table 2. Research question statement based on PCC approach

Scoping review research question statement following PCC approach	
Population	Canine and equine patients, their owners/caregivers, other professionals and the osteopaths treating canine and/or equine patients
Concept	Breathing patterns and neurological control mechanisms of the equine and canine diaphragm during tidal breathing
Context	The existing knowledge about the general characteristics of breathing patterns and neurological control of the equine and canine diaphragm during tidal breathing

4.2.1 Search strategy and eligibility criteria

According to Peters et al (2020: 422) scoping reviews usually have less restrictive inclusion criteria which enables the broader extent in comparison to systematic or sys-

tematized reviews. Hadie (2024: 187) highlight that the specification the types of participants, concepts, contexts and sources will increase the comprehensiveness of the scoping review protocol.

Peer-reviewed complete studies and reviews in English related to the breathing pattern and neural control mechanisms of canine and equine diaphragm during tidal breathing were included. Databases do not always search the full text, so an additional hand-search from journals and reference lists of chosen articles was done. Data searches were conducted without date restriction. Non-peer reviewed data such as book chapters, theses, dissertations and websites were excluded from the data sources. First selection was be done at title level, then at the abstract level and lastly at the full text level.

A preliminary search was carried out in ProQuest Central database on March 2025, using the following terms for the title, abstract and keywords (where applicable): (diaphragm AND equine OR canine (configuration OR anatomy OR anatomic* OR function OR function* OR neural control OR neural control* OR innervation) AND tidal breath* OR tidal breathing). After the preliminary search the keywords and index terms used in the initial findings were analyzed to refine the search strategy. The following step was a comprehensive search after refining the keywords and index terms in the ProQuest Central, Science Direct and Wiley Online Library databases. The search strategy was documented, and extracted data was charted in table form including the essential information about the data. The detailed data search process can be found from Appendix 1.

The final data searches according to the refinements suggested by the librarian were carried out in ProQuest Central, Science Direct and Wiley Online databases on March 2025. The applied search statement was following for ProQuest Central: (diaphragm OR "respiratory muscles") AND noft(equine OR canine OR dog OR horse) AND ("tidal breath*" OR "mechanics of breathing"). Whereas the applied search statement was following for Science Direct and Wiley Online Library: (diaphragm OR "respiratory muscles") AND (equine OR canine OR dog OR horse) AND ("tidal breath" OR "mechanics of breathing"). The search was refined by peer-reviewed filter and only results in English language was included.

4.2.2 Study selection and critical appraisal

Altogether the database searches provided 348 results. The data was managed with Zotero software and exported to Rayyan (Rayyan QCRI application 2025) which is AI-powered Systematic Review Management Platform. The data was downloaded to Zotero software first and organized in three folders corresponding the database where the results were from. From Zotero the data was uploaded to Rayyan where the title, abstract and finally full text level screening was performed by the author of this thesis. The whole process of study selection can be seen in Figure 1. The phases of the selection of articles mapped out according to PRISMA 2020 flow diagram for new systematic reviews which included searches of databases, registers and other sources.

The duplicates (n=4) and articles (n=13) not fulfilling the inclusion criteria; including congress abstracts, reference lists and indexes were removed before screening in title level. The remaining 331 articles were screened on title level, from which 199 articles were excluded due not fulfilling the inclusion criteria. Remaining 132 articles were screened on abstract level in April 2025 from which 75 were excluded due to not fulfilling the eligibility criteria.

The remaining 57 articles were sought for retrieval in April 2025 from which 24 were not available as full text version from Metropolia UAS databases. The full text versions of the 33 articles were downloaded successfully and screened at full text level. Three of these 33 records were excluded due to being wrong publication type (online reference work chapter based on the original article). Consequently, the librarian from Metropolia UAS library was consulted to find possible ways to access missing 24 articles. One of the articles was accessible as long-distance loan and was printed at library of Myllypuro campus of Metropolia UAS from where it was sought as a printed version and screened at full text level.

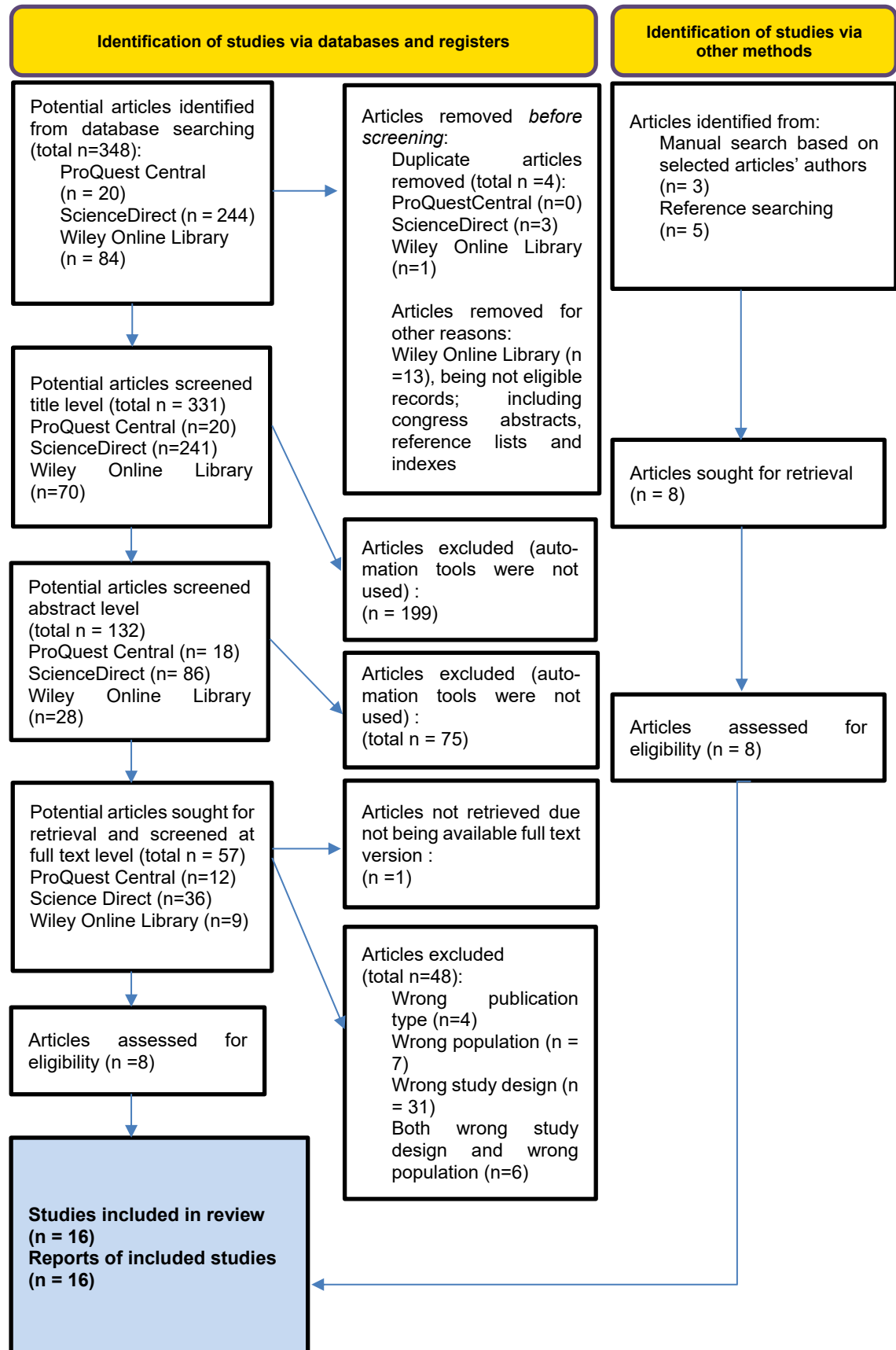
The missing articles were sought for retrieval from Helsinki University library, precisely via Helka database's access to international articles in April 2025, as advised by the librarian. Majority (22) of these 23 articles were available and were screened at full text level in April 2025. One of the missing articles was not available from Helka either, so it was excluded from full text screening.

After the whole process of full text level screening 48 articles were excluded due to having 1) wrong population(n=7); 2) wrong study design(n=31); 3) both wrong popula-

tion and study design (n=6) or 4) wrong publication type (n=4). The remaining eight articles were chosen to be initially included in the review based on the screening (title, abstract and full text) process. Additional hand search was performed to find any undetected articles related to the research questions based on the authors of initially chosen articles. Consequently, additional eight manually searched articles were sought for full text retrieval.

Finally, 16 articles were initially included in the analysis phase. Potential ethical issues may occur in literature reviews regarding study selection and interpretation of the results. Therefore, critical appraisal of the selected studies by using the Joanna Briggs Institute (JBI) critical appraisal tools was conducted to improve the overall validity and transparency of this scoping review. The critical appraisal process of this study is described in chapter 4.3. Scoping review quality assessment.

Figure 1. The phases of the selection of articles mapped out according to PRISMA 2020 flow diagram for new systematic reviews which included searches of databases, registers and other sources.



4.2.3 Data extraction and synthesis

Data from the selected articles were extracted and synthesized using thematic analysis. Thematic analysis was chosen as an analyzing method for the results from this scoping review. Thematic analysis is applicable to various theoretical frameworks, and it provides approachable and systematic method for code and theme generation from qualitative data. Thematic analysis aims not only to summarizing of the gathered data, but also to identifying and interpreting the key features of the data. (Braun & Clarke 2016:288.) Consequently, it was a suitable analysis method for analyzing data from relatively unexplored topic.

Thematic analysis is described by Braun & Clarke (2016:288) as a method for identifying, analyzing, and interpreting patterns of meaning within qualitative data. In this master's thesis, an immersing approach was adopted to gain deeper understanding of the data. According to original authors the reflexive thematic analysis is about "the researcher's reflective and thoughtful engagement with their data and their reflexive and thoughtful engagement with the analytic process" (Braun and Clarke 2019, p. 594). The analysis process was chosen to be inductive, in which the codes are produced merely reflective of the content of the data, free from pre-conceived conceptual framework. (Byrne 2022: 1396). The inductive approach lets the data to speak for itself with a notion to remain committed to the research questions.

According to Braun & Clarke (2006:87) the phases of thematic analysis can be seen as following six-phase framework:

- Phase 1: Familiarization with the data
- Phase 2: Initial code generation
- Phase 3: Theme searching
- Phase 4: Theme reviewing
- Phase 5: Theme definition and naming
- Phase 6: Creating the report

4.2.4 The process of code generation

The codes were extracted from the data, and the themes were constructed from them. Primarily, the analysis phase followed the strategy of thematic analysis according to Braun & Clarke (2006). However, the chosen approach in this Master's thesis aimed to comply the reflexive approach to thematic analysis because it encourages the researcher's operative role in knowledge construction. (Byrne 2022: 1393). Codes were revised several times to reach new patterns of meanings during the analytical process. The table including all the initial codes can be found from the Appendix 3 (The initial codes of the thematic analysis).

Table 3. Three examples of the initial codes and their definitions

Codes	Definitions
Resting volume reflects the physical equilibrium	<p>A point of physical equilibrium during respiration where forces from the outward recoil of the chest wall and the inward recoil from lungs are counteracted. The relaxation volume is a state where respiratory muscles are passive. Thus, the outward recoil depends on the elastic characters of the rib cage, and the inward recoil depends on the viscoelastic properties of the lung which are determined by the lung tissue properties and the alveolar tendency to collapse. The collapsing pressure results from the surface tension at the alveolar air-fluid interface.</p> <p>In horse the resting volume is greater than functional residual capacity which is different from majority of mammals.</p> <p>In dog the resting volume and functional residual capacity are very close or equal.</p>

<p>Polyphasic tidal breathing pattern has varying components of active and passive phases</p>	<p>During the inspiration and/or expiration clear peaks in airflow and respiratory muscle activation are detected and consequently the breathing pattern is bi-, or triphasic depending on the number of detected peaks.</p> <p>Biphasic breathing pattern is the chosen breathing pattern in a healthy, adult horse.</p> <p>The demand of O₂ increases when fleeing a predator which results in increase of the active component of expiratory phase and expiratory muscle recruitment, and compulsion of the lungs below the relaxation volume follows. Thus, increase in ventilation is achieved if the breathing frequency does not decrease.</p>
<p>Monophasic tidal breathing pattern has economical advantages</p>	<p>During the inspiration and expiration no peaks of airflow or respiratory muscle activation are detected, therefore the airflow is monophasic during both inspiration and expiration. This breathing pattern is chosen by foals under year of age and dogs, as well as the most of other terrestrial mammals.</p>

4.2.5 Theme construction

Six main themes were constructed based on the codes and subthemes identified during the analysis of selected studies. These themes and their corresponding subthemes are presented later in the results section (specifically in chapters 5.1 to 5.3) according to the research questions.

The first section presents the general characteristics of the equine and canine breathing pattern (see chapter 5.1 The general characteristics of the equine and canine breathing pattern). This chapter responds to the first (*What are the general characteristics of the equine and canine breathing patterns during tidal breathing?*) and the first

part of the third (*What are the essential species-related similarities and differences in the breathing patterns between equine and canine diaphragm during tidal breathing?*) research question. The following themes are included in this section:

- 1) Metabolism is the primary motor for gas exchange (see chapter 5.1.1)
- 2) Physical properties of the respiratory system in both equine and canine species (see chapter 5.1.2)
- 3) Parts of the tidal breathing pattern (see chapter 5.1.3)

The second section describes the neurological control mechanisms of the equine and canine diaphragm during tidal breathing. (see chapter 5.2 The neurological control mechanisms of the equine and canine diaphragm during tidal breathing) This chapter responds to the second research question (*How is the equine and canine diaphragm neurologically controlled during tidal breathing?*). The following theme is included in this section:

- 1) The respiratory control during tidal breathing (see chapter 5.2.1)

The third section evaluates the differences in the breathing pattern of the equine and canine species during tidal breathing. (see chapter 5.3 The species-related differences of the equine and canine breathing pattern during tidal breathing) This chapter responds to the second part of the third (*What are the essential species-related similarities and differences in the breathing patterns between equine and canine diaphragm during tidal breathing?*) research question. The following themes are included in this section:

- 1) Differences in species-related physical properties of the respiratory system (see chapter 5.3.1)
- 2) Individualized blueprint for the optimal tidal breathing pattern (see chapter 5.3.2)

4.3 Scoping review quality assessment

According to Peters et al (2022:954) the main goal of a scoping review is to report and map a body of literature in terms of elements and details determined by the review's

objective, research questions and inclusion criteria and therefore the critical appraisal of the sources of evidence is often left out. However, a detailed plan for the conduct and reporting should be included in the scoping review protocol to improve transparency and focus of the whole process. (Peters et al 2022:955).

In this master's thesis the quality assessment of the eligible studies was conducted according to the quality assessment criteria of the Joanna Briggs Institute (JBI). The PRISMA extension for scoping reviews including the checklist of 20 essential and 2 additional items and tips sheets for each item was used throughout the process of conducting this scoping review.

The quality of the selected articles was assessed after the study selection had been completed. The critical appraisal checklists were chosen according to the methodological approach of each chosen article, which included 5 narrative reviews, 10 quasi-experimental studies and 1 expert opinion. None of the articles were excluded due to poor overall quality. Each question of the checklist was given a grading of one point for positive answer (1 for "yes", 0 for "no") and final points are shown in the last column of the table including the details of extracted data in Appendix 2. The summary of data from selected articles including the quality assessment.

5 Results

From the 16 articles selected for the review three were from Australia, two from Belgium, two from Canada, five from the United States of America and one from Italy. Two of the articles were from more than one country: from both Canada and United States of America. The articles represented several methodological approaches, from which the majority (n=10) were quasi-experimental studies, five narrative reviews and one expert opinion. Publication year range was from 1982 to 2019.

Based on the quality assessment, all of the narrative reviews (n=5) and one expert opinion were assessed as high-quality data prepared by the specialized researchers with years of experience from their field of study. Whilst the quality assessment of the quasi-experimental studies (n=10) ranged from 4 out of 9 points to 8 out of 9 points. Hence, the scored points of the quasi-experimental studies had the mean value of 6,3 of 9 points. Majority of these studies did not have control groups or follow-up recordings which immediately affected to the scoring of the quality assessment. Many of the quasi-experimental studies lacked the ethical permission statement although experiments for animals were conducted in them. The scores of each article are stated in Appendix 2. The summary of data from selected articles including the quality assessment. None of the articles were omitted from the analysis after the critical appraisal. This was a conscious decision by the author of this study with the goal to acquire as broad view to the subject as possible.

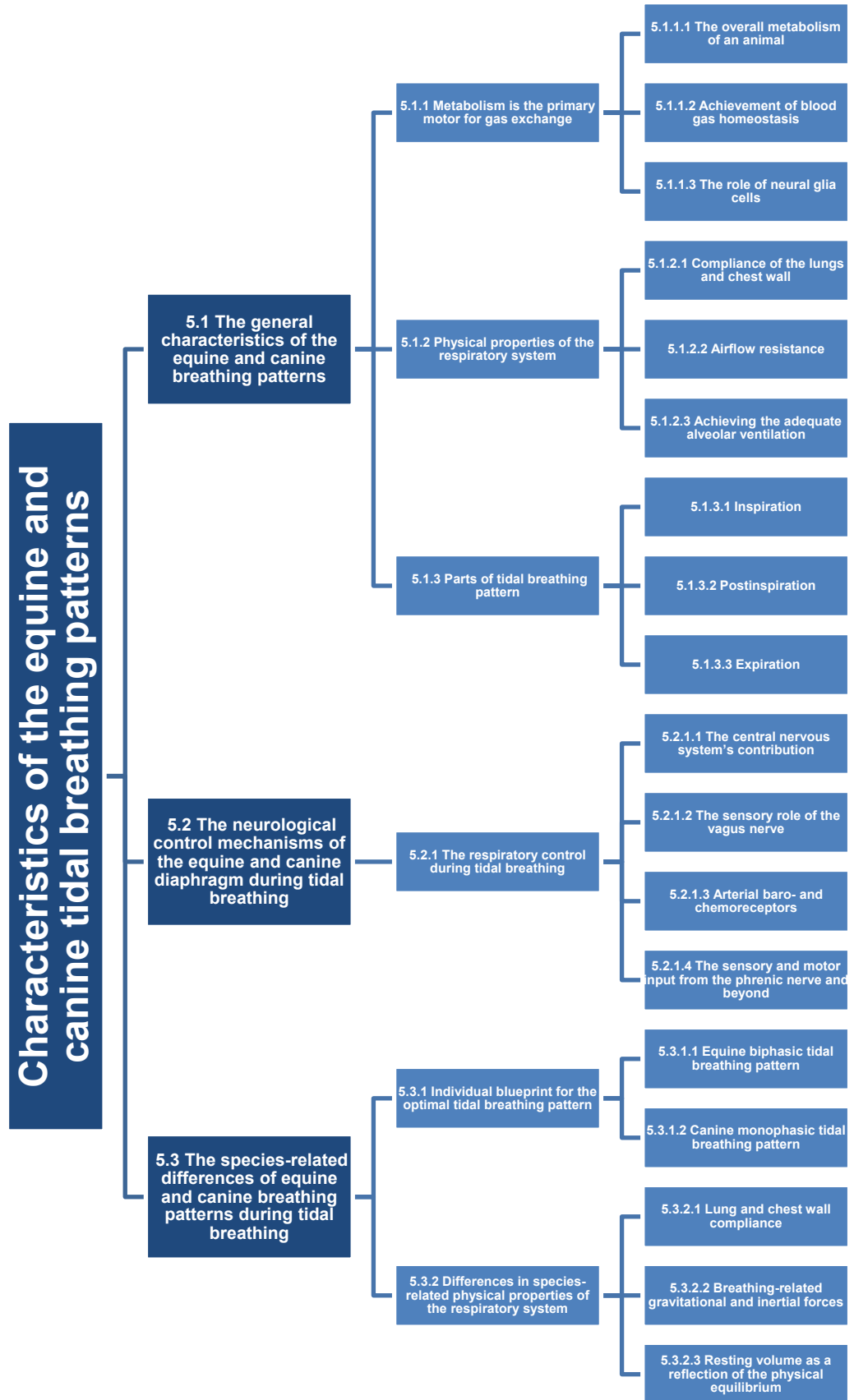


Figure 2. Characteristics of the equine and canine tidal breathing patterns. The division of the six main themes (in the middle) and subthemes (the column at right) arranged according to the three research questions of this study (in dark blue) with numbers of the corresponding chapters.

5.1 The general characteristics of the equine and canine breathing patterns

The general characteristics and the *similarities* of equine and canine breathing patterns during tidal breathing are described in this section. Thus, the content of this section is related to both research questions 1) What are the general characteristics of the equine and canine breathing patterns during tidal breathing? and 3) What are the essential species-related similarities and differences in the breathing patterns between equine and canine diaphragm during tidal breathing?. For clarity, the species-related *differences* between the equine and canine breathing patterns are described separately in chapter 5.3 (The species-related differences of the equine and canine breathing patterns during tidal breathing).

5.1.1 Metabolism is the primary motor for gas exchange

Firstly, the chosen breathing pattern during tidal breathing is a consequence of the current metabolic demand determined by the homeostatic processes of the animal. Moreover, it is important that the work of breathing is as economical as possible and therefore the blood gas balance needs to be achieved with minimal respiratory work. Thirdly, for the neural control of the respiratory system to function properly, the glial cells contribute to the maintenance of adequate internal environment surrounding the neurons within the body of an animal. Furthermore, continuous breathing requires a significant metabolic input as the respiratory muscles are the only skeletal muscles which remain active during sleep and awake states from birth to death. (Mortola 2019:52; Del Negro, Funk & Feldman 2018: 353.)

This chapter describes the first one of the main themes (*Metabolism is the primary motor for gas exchange*), and the following three subthemes included in this main theme.

- The overall metabolism of an animal determines the need for ventilation (chapter 5.1.1.1)
- Achievement of blood gas homeostasis (chapter 5.1.1.2)
- The role of neural glia cells as a metabolical support for respiratory neurons (chapter 5.1.1.3)

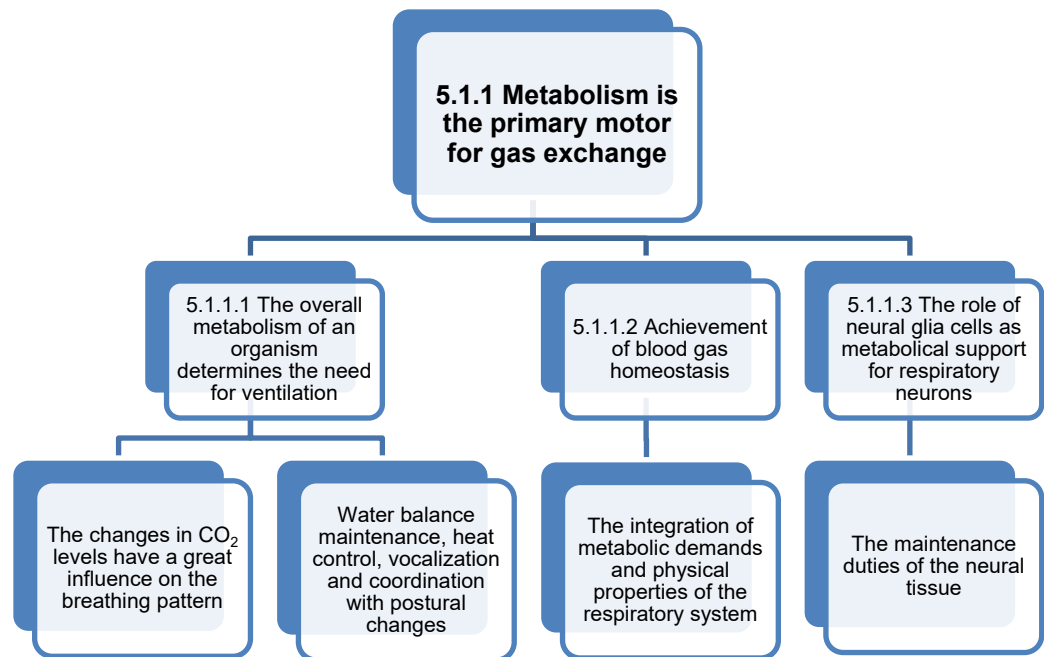


Figure 3. The metabolism as the primary motor for gas exchange including the subthemes (see subchapters 5.1.1.1 to 5.1.1.3)

5.1.1.1 The overall metabolism of an animal determines the need for ventilation

At rest, above all, the most important factor in determining the need for ventilation and the resulting breathing pattern is the overall metabolism. The sufficient gas exchange results from pulmonary ventilation which is a product of breathing frequency, and the amount of air inhaled with each breath. (Mortola 2019: 48). Even at rest, during tidal breathing, continuous metabolic processes require adequate contribution of ventilation. These processes include the very basic functions of an organism, such as water balance maintenance, heat control, vocalization and coordination with postural changes. (Del Negro, Funk & Feldman 2018:353).

5.1.1.2 Achievement of blood gas homeostasis

To minimize the cost of the metabolic demands of the body the adopted breathing pattern needs to correspond to the physical properties of the respiratory system (see the following chapter 5.1.2 Physical properties of the respiratory system in both equine and canine species). The equines and canines, both mammalian species, do not differ significantly in the regards of metabolism. Carbon dioxide (CO₂) is one of the byproducts of the cellular metabolism of an animal. The changes in CO₂ levels have a great influence on the breathing because of its direct effect on the pH of an organism. However,

the same is not the case with the change in the levels of O_2 , which does not provoke immediate changes in the breathing pattern. (Del Negro, Funk & Feldman 2018:353). The blood and cerebrospinal fluid concentration of these vital gases is continuously monitored by chemoreceptors (see chapter 5.2.1.1 The central nervous system's contribution and 5.2.1.2 The sensory role of the vagus nerve).

Moreover, the tidal breathing pattern of most terrestrial mammals also contributes to the minimal metabolic consumption by election of active inspiratory phase and passive expiratory phase (see more from chapter 5.1.3. Phases of the tidal breathing pattern). Nevertheless, exceptions exist since the tidal breathing pattern of the equine species differs from this most chosen pattern (see more chapter 5.3.1 Individualized blueprint for the optimal tidal breathing pattern). (Del Negro, Funk & Feldman 2018: 353; Mortola 2019: 51.)

5.1.1.3 The role of neural glia cells as metabolic support for respiratory neurons

Moreover, even the neurological control mechanisms require properly functioning metabolism. Consequently, the nervous system does not contain only the neurons but also great number of cells responsible for the 'cleaning and household' duties (i.e. metabolic waste transport and chemical stability maintenance). The glial cells are one type of these cells with significant maintenance properties. Significant contribution from the glial cells to the maintenance of homeostasis of the neural tissue is achieved by participating in the metabolic processes within the brainstem. (Del Negro, Funk & Feldman 2018:360). (see more chapter 5.2.1.1 The central nervous system's contribution) Thus, they facilitate the proper function of the breathing.

5.1.2 Physical properties of the respiratory system in both equine and canine species

The physical properties of the respiratory system contribute significantly to the outcome of the whole breathing pattern phenomenon. The respiratory system including the lungs, airways and chest wall have all their proportional physical properties. In this study, the physical properties are defined as: 1) the elasticity (i.e. compliance) of the lungs and chest wall; 2) the alveolar tensional properties the forces related to surface tension; and 3) the tonus of the airway smooth muscles at the conducting airways. However, breathing is an active phenomenon and therefore not only determined with the physical properties of the respiratory system. (Frappell & MacFarlane 2005: 144). The species-related differences in physical properties of the respiratory system between equine and canine species are described in detail later in results section (see

chapter 5.3 The species-related differences of the equine and canine breathing pattern during tidal breathing).

This chapter describes the second one of the main themes (*Physical properties of the respiratory system in both equine and canine species*), and the following three sub-themes included in this main theme.

- Lung and chest wall compliance (chapter 5.1.2.1)
- Airflow resistance created by the smooth muscles of the airways (chapter 5.1.2.2)
- Achievement of the adequate alveolar ventilation (chapter 5.1.2.3)

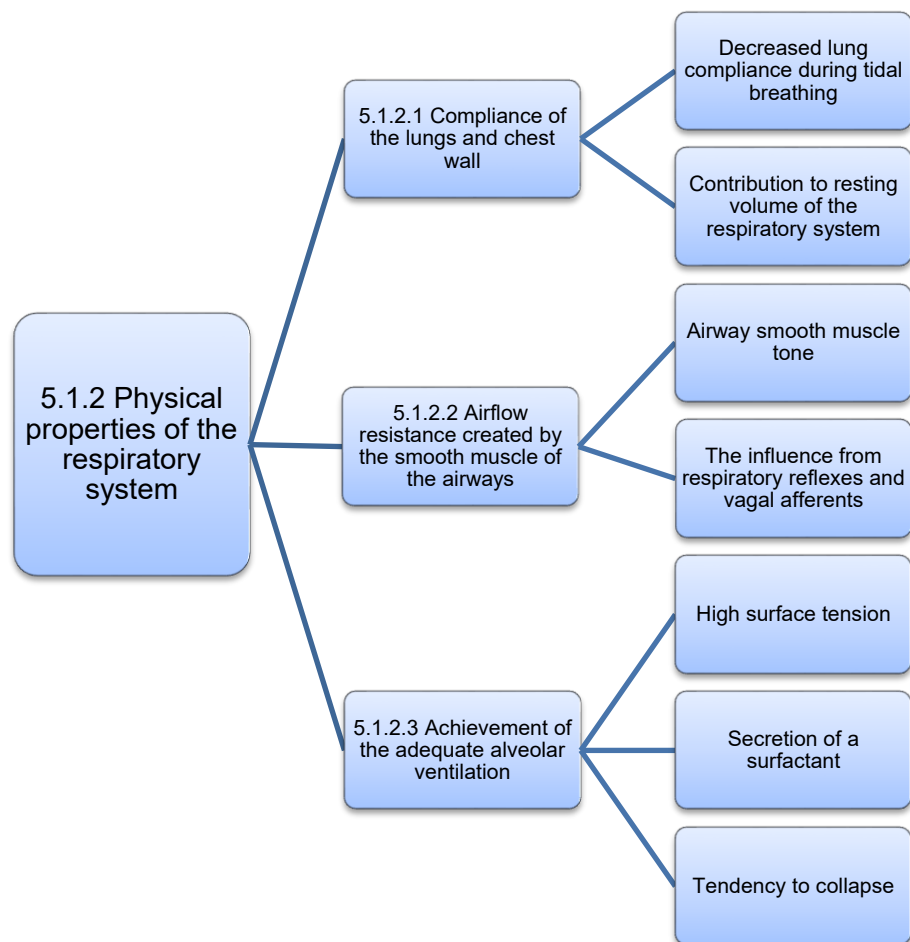


Figure 4. Physical properties of the respiratory system in both canine and equine species including the subthemes (see subchapters 5.1.2.1 to 5.1.2.3)

5.1.2.1 Compliance of the lungs and the chest wall

Lung compliance can be defined as the elasticity of lungs. During tidal breathing the lung compliance decreases because the small lung units tend to collapse due to the removal of surfactant from the inner surface of the alveolae and bronchioles (see in further detail in chapter 5.1.2.3 Achievement of the adequate alveolar ventilation). (Yu 2005: 220). Decreased lung compliance during tidal breathing is reversed by the regular single deep breaths, or sighs. During the sighs, the breathing pattern is altered due to sudden changes in lung compliance, because the slowly adapting stretch receptors (SARs) and the rapidly adapting stretch receptors (RARs) within the airways become activated (see more chapter 5.2 The neurological control mechanisms of the equine and canine diaphragm during tidal breathing). (Fisher & Sant'Ambrogio 1985:122.)

Compliance of the chest wall can be defined as the elastic characteristics of the thorax, abdomen and diaphragm, which are the structures that move during lung inflation and deflation. The compliance of the lungs and chest wall contributes to the resting volume of the respiratory system which has a consequent effect to the tidal breathing pattern of an animal (see more chapter 5.3.2.3 Resting volume as a reflection of the physical equilibrium). Possibly, the viscoelastic properties of the tissues are also responsible for the sensory receptor behavior. (Yu 2005:233). Thus, the dynamical or static changes in physical properties of the respiratory system may also account for the changes in neural receptor sensitivity.

5.1.2.2 Airflow resistance created by the smooth muscles of the airways

The airway smooth muscle tone has an effect not only to lung compliance but also to airflow resistance and therefore affects to the chosen breathing pattern. The airway smooth muscles are the smooth muscle layer on the surface of the conducting airways (at the main bronchi and bronchioles), whose contraction results in the constriction of the bronchi (i.e. bronchoconstriction). On the contrary, their relaxation results in dilation of the bronchi (i.e. bronchodilatation). The ventilatory dead space (the inhaled air staying in the conducting airways and hence not contributing to alveolar gas exchange) is decreased, and airflow resistance increased when the smooth muscles of airways are contracted. The effects from bronchoconstrictor and bronchodilator reflexes influence the basic tone of airway smooth muscles. Moreover, the airway smooth muscle tone is maintained by the central chemoreceptors at the level of the brain stem reacting to e.g. arterial CO₂ levels, and the efferent tone of the vagal branches. (Coleridge & Coleridge 1989:3; Fisher & Sant'Ambrogio 1985:121; Yu 2005:236.)

The perceived sensory stimulus from surprisingly far distance from the respiratory system may have an influence on the airway smooth muscle tone, and thus on regulation of the breathing pattern. Sensory areas remote to the respiratory tract may also contribute to bronchomotor reflexes, such as arterial chemo- and baroreceptors (see chapter 5.2.1 The control mechanisms of the diaphragm during tidal breathing), and from sensory nerve endings in the gut, skin, heart and skeletal muscles. (Coleridge & Coleridge 1989:3).

5.1.2.3 Achievement of the adequate alveolar ventilation

Alveolae, as fluid-lined structures have high surface tension at the air-water interface on their surface, which needs to be exceeded by very high inspiratory pressure. In turn, secretion of a type of biofilm, the lung surfactant, on the surface of the alveolae lowers the high surface tension. The alveolae tend to collapse at the end of each the expiration during tidal breathing due to spontaneous removal of the surfactant. The low transpulmonary pressure combined with low lung volume increase the alveolar collapsing tendency. Regular sighs are required to reinflate the collapsed alveolae, to restore the surfactant to the surface biofilm of the alveolae and to prevent atelectasis (the collapse of a part of a lung) during tidal breathing. (Frappell & MacFarlane 2005: 146; Del Negro, Funk & Feldman 2018:356; Fisher & Sant'Ambrogio 1985:123.)

Consequently, the larger inspiratory efforts (i.e. sighs) belong to the normal breathing pattern. Sighs may occur in higher frequency in young mammals or during hypoxia when the atelectasis have higher tendency to occur due to increased breathing frequency. The emotions, such as relief, exhaustion, grief or happiness may provoke higher sighing frequencies during tidal breathing. (Del Negro, Funk & Feldman 2018: 362). Rapidly adapting stretch receptors (RARs) (see chapter 5.2.1.2) are suggested to contribute into the generation of sighs due to increase in their activity when lung compliance is reduced during deflation of the lungs. (Fisher & Sant'Ambrogio 1985:122).

5.1.3 Parts of tidal breathing pattern

In general, the tidal breathing pattern in mammals always consists of inspiration, often postinspiration and sometimes active expiration in certain species, such as is equines (see more chapter 5.3.1.1 The equine biphasic tidal breathing pattern). Furthermore, the state of an animal affects the phasic composition of the tidal breathing pattern. In

long term, the injuries, growth and maturation, ageing, disease and pregnancy also influence the adoption of certain tidal breathing pattern. (Del Negro, Funk & Feldman 2018:351.)

This chapter describes the third one of the main themes (*Phases of tidal breathing pattern*) and the following three subthemes included in this main theme.

- Inspiratory muscle contraction is a key feature of mammalian breathing (chapter 5.1.3.1)
- Benefits of postinspiration (chapter 5.1.3.2)
- Expiration (chapter 5.1.3.3)

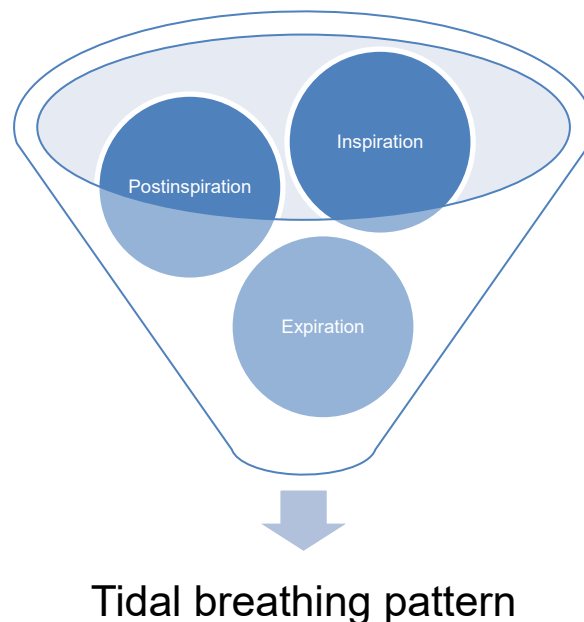


Figure 5. The typical parts of tidal breathing pattern (see more from subchapters 5.1.3.1 to 5.1.3.3)

5.1.3.1 Inspiratory muscle contraction is a key feature of mammalian breathing

Inspiratory muscle contraction is a key feature of mammalian breathing. The present view suggests that the inspiration is the inexorable phase of the breathing cycle, while postinspiration and expiration are dependent. (Del Negro, Funk & Feldman 2018: 351.) It is defined as the phase of respiratory activity where the lungs are inflated, the peak of diaphragmatic muscle activity is recorded, the intra-abdominal pressure increases, and the intrathoracic pressure decreases. (Koterba, Kosch, Beech & Whitlock 1988:343). Inspiration may include active and/or passive components depending on the chosen

breathing pattern of an individual. The rhythm of inspiration has its origins at the medullary microcircuit, preBötzinger Complex (see chapter 5.2.1.1 The central nervous system's contribution) (Del Negro, Funk & Feldman 2018: 351).

5.1.3.2 Benefits of postinspiration

Postinspiration is often manifested in many mammals. This phase occurs immediately after inspiration and consists of shortening of the laryngeal adductor muscles resulting in increase of airway resistance, and extension of the contraction of the diaphragm, which hinders the lung deflation. Most likely the vagal afferent mechanoreceptors (see chapter 5.2.1.2 The sensory role of the vagus nerve) have a significant role in the regulation of both the regulation of the laryngeal adductor recruitment and the post-inspiratory activity of the muscles of inspiration. (Del Negro, Funk & Feldman 2018: 356.) In the equine species some postinspiratory activity of the diaphragm has been recorded during the first phase of expiration. (Koterba et al 1988:343). Detailed information about the possible postinspiratory phase of canines was not found during the analysis of data included in this scoping review.

Postinspiratory phase profits the alveolar gas exchange by lengthening the amount of time that inspired air stays in the lungs and reduces the probability of airway collapse by assisting laminar expiratory airflow during expiration. Postinspiration is not obligatory part of the breathing cycle or essential for tidal breathing since it does not occur during sleep or anesthesia. (Del Negro, Funk & Feldman 2018:356.)

However, in equines the post-inspiratory activity of diaphragm and other inspiratory muscles may also be capable of counteracting the passive inward recoil of the respiratory system. Additionally, postinspiration may contribute to the prevention of sudden transition from inspiration to expiration (Koterba et al 1988:343, 344.). Later, in chapter 5.3.2.3 the passive inward recoil is discussed in detail.

5.1.3.3 Expiration

In mammals, the expiration is usually passive during tidal breathing, which is possibly related to appearance of the diaphragm during evolution resulting in more efficient tidal breathing pattern (Del Negro, Funk & Feldman 2018:353). Expiration is defined as the phase of respiratory activity where the lungs are deflated (not completely), the intra-abdominal pressure decreases, and the intra-abdominal pressure increases. Expiration

may include active and/or passive components depending on the chosen tidal breathing pattern of an individual. The biphasic tidal breathing pattern typical for equines often includes active components of expiration and is described later in chapter 5.3.1.1.

5.2 The neurological control mechanisms of the equine and canine diaphragm during tidal breathing

The neurological control mechanisms of the equine and canine diaphragm are described in this chapter. Therefore, the content of this chapter is related to the research question 2) How is the equine and canine diaphragm neurologically controlled during tidal breathing?. The ventilation results from the conversion of the neural output to the respiratory movement by the lungs and chest wall. Remarkable differences in the neural control mechanisms between the equine and canine species were not found during the analysis of the selected articles apart from the motoric innervation to the two parts of the diaphragm in dogs. (see chapter 5.2.1.4 The sensory and motor input from the phrenic nerve and beyond) Consequently, the features of the respiratory control of both equine and canine species during tidal breathing are described together in the following subchapters.

5.2.1 The respiratory control during tidal breathing

The control mechanisms involved in respiratory pattern generation have their foundation on the interconnections between several neural structures. These structures consist of not only the central sensory-, motor- and metabolism-related structures at the level of brainstem, but also the peripheral afferent (i.e. sensory) and efferent (i.e. motor) nerve fibres. The adoption of optimal tidal breathing pattern requires well-functioning coordination between the proprioceptors of the chest wall, sensing muscle length and force, and lung mechanoreceptors, monitoring absolute and tidal changes in lung volumes which are both integrated in the central nervous system. (Mortola 2019: 52).

This chapter describes the fourth one of the main themes (*The respiratory control during tidal breathing*) and the following four subthemes included in this main theme.

- The central nervous system's contribution (chapter 5.2.1.1)
- The sensory role of the vagus nerve (chapter 5.2.1.2)
- Arterial baro- and chemoreceptors (chapter 5.2.1.3)
- The sensory and motor input from the phrenic nerve and beyond (chapter 5.2.1.4)

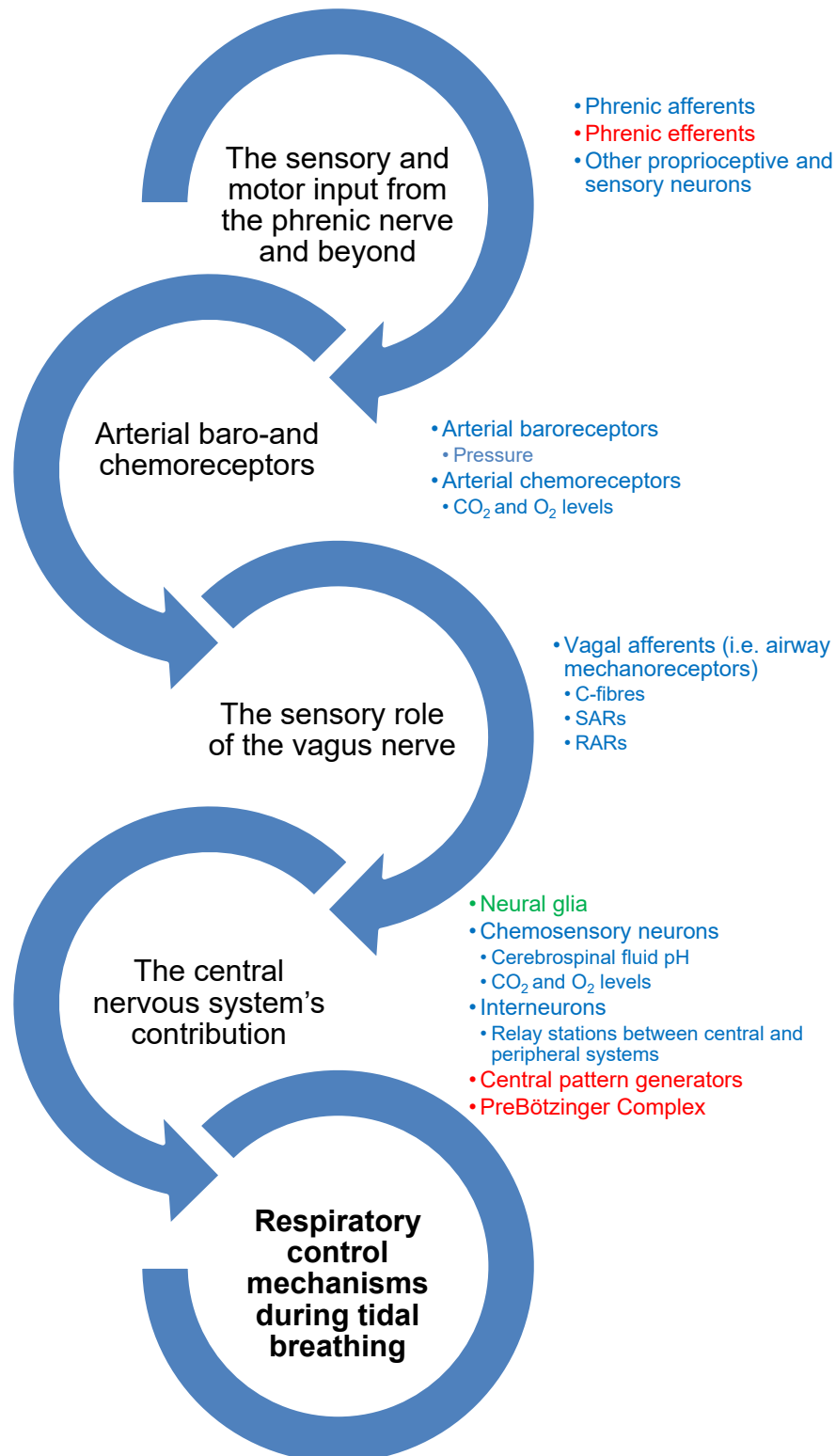


Figure 6. The respiratory control mechanisms during tidal breathing (Structures related to afferent (i.e. sensory feedback) in blue, efferent (i.e. motor command) in red and metabolic maintenance (i.e. modulation of ion concentrations and response to and release of neurotransmitters) in green.

5.2.1.1 The central nervous system's contribution

During tidal breathing, the control of the diaphragm is a consequence of a complex array of neural impulses from both sensorial feedback from the various tissues of the body to the central nervous system, and motoric commands from the brainstem to the respiratory-related muscular structures. The contractions of these muscular structures provide movements resulting in changes of airflow and intrathoracic and intra-abdominal pressure, which finally results in well-functioning respiratory movement. (Frappe & MacFarlane 2005:143; Del Negro, Funk & Feldman 2018: 353.)

The central respiratory-related processes in the brainstem involve the neural glia cells (e.g. astrocytes), central chemoreceptors, respiratory-related central pattern generators (CPGs) and inspiration related neural microcircuit, the preBötzinger Complex (preBötzc). Additionally, within the brainstem chemosensory neurons and glia cells react to changes in pH, O₂ and CO₂ levels in the blood and the cerebrospinal fluid and transmit the synapses to the preBötzc and respiratory-related areas to maintain the homeostasis of an organism. (Del Negro, Funk & Feldman 2018: 353; Coleridge & Coleridge 1989: 44.) The role of the neural glia cells has been discussed earlier in the results section. (see chapter 5.1.1.3 The role of neural glia cells as a metabolic support for respiratory neurons)

Moreover, inspiration, postinspiration and expiration are driven by three distinct, coupled oscillators in the brainstem. When all three phases are displayed, the preBötzc in the medullar part of the brainstem conducts the coordination of the phases. Interneurons act as a relay between the input from the stretch receptors of the lungs and inspiratory preBötzc. Consequently, the rhythmical inhibition of inspiratory preBötzc and excitation of expiratory-initiating lateral parafacial nucleus (pF) results in alternating inspiration and expiration. (Del Negro, Funk & Feldman 2018: 363.)

5.2.1.2 The sensory role of the vagus nerve

The vagus nerve incorporates many sensorial fibres involved in perceiving physical changes related to respiratory system. The sensorial fibres of the vagus nerve are not only located within the respiratory system but in this study the perspective is limited to them. These vagal respiratory-related sensorial fibres, the airway mechanoreceptors, (i.e. vagal afferents) have substantial significance in the maintenance of continuous breathing. The vagal afferents include three main types of receptors: slowly adapting stretch receptors (SARs), rapidly adapting stretch receptors (RARs) and respiratory C-

fibres. (Coleridge & Coleridge 1989: 11; Yu 2005: 218). Vagal denervation results in irregularities of breathing rhythm, decreased lung compliance, apnea and even respiratory failure in newborns of various species. (Frappell & MacFarlane 2005:150). During tidal breathing, the changes in lung compliance and volume are perceived by the vagal afferent receptors. Moreover, these receptors can induce reflexes which dynamically adjust the respiratory mechanics by causing alterations in the breathing pattern, tonic activity of respiratory muscles and the airway smooth muscle tone. (Fisher & Sant'Ambrogio 1984:122).

Slowly adapting stretch receptors (SARs) detecting static changes in lung mechanics have a great influence on the tidal breathing pattern in animals (is suggested to be less so in humans). The rhythmic discharge of SAR especially during the inspiratory phase of tidal breathing is the primary element of vagal afferent input from the lower respiratory tract which is integrated at the level of the brainstem. (Coleridge & Coleridge 1989:12.)

Rapidly adapting receptors (RARs) detecting dynamic changes in lung mechanics have a minor importance during tidal breathing. RARs are activated more during larger changes in lung volumes, such as during rapid deflation but also often demonstrate higher activity during the peak of the inspiratory airflow. RARs may contribute significantly to Hering-Breuer deflation reflex which occur after rapid decrease in lung volume and consists of quick termination of expiration and following augmentation of inspiration. Although traditionally observed in newborns, the greater number of RARs found adult dog in comparison to puppies supports the existence of this reflex also in mature dogs. (Fisher & Sant'Ambrogio 1984:118; Coleridge & Coleridge 1989: 49; Yu 2005: 219.)

In terrestrial mammals, SARs are greater in number than RARs, correspondingly 15% and 4% of the total airway receptors. (Fisher & Sant'Ambrogio 1984:119). Lung mechanoreceptors also have a great significance in postinspiratory phase together with pontine (i.e. located at the pons of the brainstem) circuits. (Del Negro, Funk & Feldman 2018: 356.) Both SARs and RARs depend on the lung compliance to be stimulated, which can also be interpreted from their names related to stretch (of the lung tissue they are located in). Nonmyelinated vagal afferent respiratory C-fibres also contribute in the mechanotransduction from the airways but respond changes in chemical rather than mechanical stimuli (e.g. in case of inflammation or infection). (Yu 2005: 218).

5.2.1.3 Arterial baro- and chemoreceptors

Furthermore, the peripheral arterial chemo- and baroreceptors influence greatly to the regulation of breathing. These neural receptors perceive CO₂-, O₂-, pH- and pressure-related changes within the arterial blood at the branch between internal and external carotid arteries. (Coleridge & Coleridge 1989: 44; Del Negro, Funk & Feldman 2018: 353). The carotid sinus baroreceptors inhibit both the smooth muscle tone of the airways and breathing. Whereas carotid body chemoreceptors have an excitatory effect both on breathing and the airway smooth muscle tone. (Coleridge & Coleridge 1989: 49; Yu 2005: 236.)

5.2.1.4 The sensory and motor input from the phrenic nerve and beyond

The phrenic sensory afferents from the diaphragm contribute to reducing the resistant work of breathing by evoking bronchodilatation (discussed more in chapter 5.1.2.2 Air-flow resistance created by the smooth muscle of the airways). The physiological explanation for this phenomenon remains unclear but it most likely has a metabolic origin. (Coleridge & Coleridge 1989: 53.)

The efferent (i.e. motor) activity of the phrenic nerve induces the actual contraction of the diaphragm. However, distinct activity of the costal and crural parts of the diaphragm has been recorded in dogs. The costal part receives its motoric innervation most commonly from the cranial segments (C₅-C₆) of the phrenic nerve, whereas the crural part has more caudal (C₇) distribution of the nerve fibres. This anatomical arrangement has direct functional consequences. Accordingly, the costal part has direct inspiratory (expanding) action on the lower ribcage whereas the crural part does not expand the lower rib cage notably in intact dogs. (De Troyer, Sampson, Sigrist & Macklem 1982: 36.)

The differences of segmental motor innervation of the parts of the diaphragm in horses were not explored in the data set of this study.

Arguably, the proprioceptors within the connective tissues (e.g. muscles, fascia) of the chest wall contribute to the distribution of information to the central nervous system about the breathing movement and the respiratory system's components. (Mortola 2019: 49). Additionally, changes beyond the actual lung tissue and conducting airways also contribute to the lung and airway control.

5.3 The species-related differences of equine and canine breathing patterns during tidal breathing

The breathing pattern during tidal breathing results from the main forces involved in breathing, such as the elasticity of the lungs and chest wall and contraction and relaxation of the respiratory muscles. However, these forces are subject to number of dynamic changes, including the species-related differences in the species-specific and individual form of an animal. (Art & Lekeux 1988: 301.) For instance, a small horse or dog has different characteristics than the larger one and therefore the breathing pattern is not only species-related but also most likely individual phenomenon.

The main differences of canine and equine breathing patterns during tidal breathing are related to the tissue qualities of the chest wall, gravitational and inertial factors and to the point of physical equilibrium, where the two above mentioned properties in a manner counteract each other.

5.3.1 Individualized blueprint for the optimal tidal breathing pattern

Interestingly, the chosen tidal breathing pattern of an animal seems to be a remarkably individual phenomenon. Tidal breathing pattern is a consequence of variable amounts of active and passive elements during both inspiration and expiration depending on the individual. The tidal breathing pattern can have variable number of phases. The polyphasic breathing pattern has varying components of active and passive phases, whereas the monophasic breathing pattern often consists of active inspiration and passive expiration. The first results in variable peaks of airflow whereas in monophasic breathing pattern no peaks of airflow are detected. The mammalian breathing has evolved to astonishingly economical mechanism despite variations in mechanical and anatomical elements with body size, internal loads and postnatal development. (Art & Lekeux 1988: 300; Mortola 2019:52.)

Adaptation to changes in the environment and internal milieu (i.e. internal environment of the body) of an animal often provokes changes in breathing. The timing and pattern of each breath are controlled by respiratory reflexes which have their foundation on the feedback from the vagal afferent stretch receptors (see chapter 5.2.3.) from the respiratory pump muscles and lungs. (Coleridge & Coleridge 1989:12; Yu 2005: 236; Frappell & MacFarlane 2005: 149).

This chapter describes the fifth one of the main themes (*Individualized blueprint for the optimal breathing pattern*) and the following two subthemes included in this main theme.

- Equine biphasic tidal breathing pattern (chapter 5.3.1.1)
- Canine monophasic tidal breathing pattern (chapter 5.3.1.2)

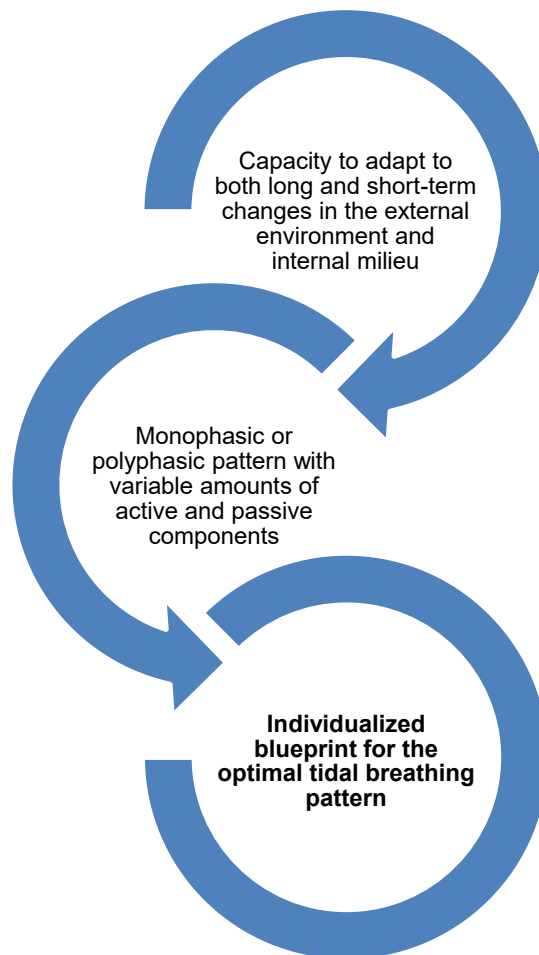


Figure 7. Individualized blueprint for the optimal tidal breathing pattern

5.3.1.1 Equine biphasic tidal breathing pattern

During tidal breathing in equine species, the first phase of inspiration seems to be primarily passive due to passive lung inflation after the relaxation of the respiratory-related abdominal muscles. The second phase of inspiration is active, and the diaphragm has a great role in it. During the first phase of the expiration, after the active phase of the inspiration the passive deflation of the lungs occur due to the relaxation of the inspiratory muscles. Subsequently, the second, active phase of the expiration is elicited

by the contraction of abdominal muscles. (Koterba et al 1988: 343.) Individually, postinspiratory activity may also be included in equine breathing pattern after the second phase of inspiration, as stated in chapter 5.1.3.2 Benefits of postinspiration.

Additionally, the biphasic tidal breathing pattern has biphasic characteristics of the air-flow measurements. During the inspiration and/or expiration clear peaks in airflow and respiratory muscle activation are detected and consequently the breathing pattern is bi-, or triphasic depending on the number of detected peaks. Biphasic tidal breathing pattern is the chosen breathing pattern in a healthy, adult horse. (Koterba et al 1988: 337; Koterba, Wozniak & Kosch 1995b: 266).

As prey animals, equine species may respond to the stimulus from the environment with an intense emotional response. The ventilation of a horse can alter rapidly due to change in emotional states (e.g. fear) resulting in variations of respiratory frequency. (Burnheim, Hughes, Evans & Raidal 2016:9). The vagal bronchomotor tone is also influenced by 'central state' (current condition of an animal) (i.e. during REM sleep). (Fisher & Sant'Ambrogio 1985:115). Consequently, the pattern of respiratory muscle activity is state-dependent.

5.3.1.2 Canine monophasic tidal breathing pattern

Monophasic tidal breathing pattern is defined as a breathing strategy in which inspiratory phase is active, and expiration occurs for the most part passively due to inward recoil of the lungs (as stated in chapter 5.1.2.3 Achievement of the adequate alveolar ventilation with minimal cost). This tidal breathing pattern has economical advantages because it decreases the energy demand to needed to overcome the elastic resistance of the lungs and chest wall. (Del Negro, Funk & Feldman 2018: 351). In this tidal breathing pattern, during the inspiration and expiration no peaks of airflow or respiratory muscle activation are detected, therefore the airflow is monophasic during both inspiration and expiration. (Art & Lekeux 1988: 300). This tidal breathing pattern is chosen in canines and in equines by foals under year of age, as well as the most of other terrestrial mammals. (Koterba et al 1995b: 271; Del Negro, Funk & Feldman 2018:351).

5.3.2 Differences in species-related physical properties of the respiratory system

In equine and canine species there are certain differences in the physical properties of respiratory system. Stiffness of the equine chest wall has certain benefits as discussed

more in the following subchapter (5.3.2.1 Differences in lung and chest wall compliance). Moreover, the point of the physical equilibrium of the respiratory system is different in these two species, which also most likely contributes to the adoption of biphasic breathing pattern in the equine species during tidal breathing.

This chapter describes the sixth one of the main themes (*Differences in species-related physical properties of the respiratory system*) and the following three subthemes included in this main theme.

- Differences in lung and chest wall compliance (chapter 5.3.2.1)
- Breathing-related gravitational and inertial forces (chapter 5.3.2.2)
- Resting volume as a reflection of the physical equilibrium (chapter 5.3.2.3)

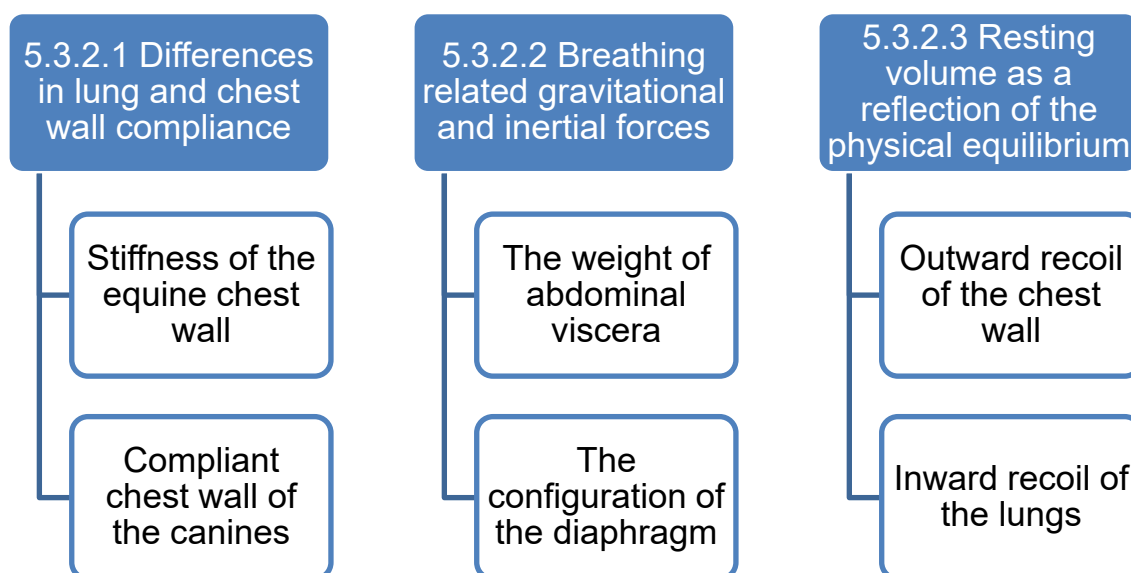


Figure 8. Differences in species-related physical properties of the respiratory system including the corresponding subthemes (see subchapters 5.3.2.1 to 5.3.2.3)

5.3.2.1 Differences in lung and chest wall compliance

Equine species seem to have very stiff chest wall in comparison to other species, even when normalized to body weight. However, the lung elasticity seems to be similar to other species. The decrease of chest wall compliance during equine development from foal to adult contributes to passive maintenance of functional residual capacity (FRC) by increasing the stiffness of the chest wall and therefore having greater resistance to the inward recoil of the lungs. (Koterba et al 1988:344.) Functional residual capacity is the amount of the air staying in the lungs after the regular, passive expiration.

The stiffness of the equine chest wall contributes to adoption of biphasic tidal breathing pattern. In a large animal, the stiff chest wall possibly serves the locomotor function and is advantageous in stabilization of end-expiratory lung volume during changes of posture. (Koterba et al 1988:344). However, the stiffness of the equine chest wall requires more elastic work of breathing, which possibly results in adoption of the biphasic tidal breathing pattern to decrease the metabolic cost of the respiration.

Whereas in canine species more compliant chest wall (among other anatomical characteristics, see the following chapter 5.3.2.2) results in active inspiration and passive expiration during tidal breathing. The changes in lung volume contribute to the activation of the costal and crural diaphragm in canines during tidal breathing via the amount of force elicited through the zone of apposition (i.e. the region where the diaphragm is directly connected to the inner surface of the lower ribcage). (Decramer, De Troyer, Kelly & Macklem 1984:1489). In canines the adequate pressure environment within the thoracic and abdominal cavities supports the optimal function of the diaphragm, resulting in well-functioning force transmission within the two parts of this muscle. (De Troyer et al 1984: 32).

5.3.2.2 Breathing-related gravitational and inertial forces

The configuration of the equine diaphragm and the weight of the visceral mass differs from the canines. The equine diaphragm domes deeply forward and is laterally compressed in accordance with the shape of the thorax. This configuration results in more ventrocranial alignment of the diaphragm in horse, and therefore a major part of the large colon and the liver fit into the cavity formed by the diaphragm. This arrangement has physical consequences to the function of diaphragm by resulting in facilitation of the lung inflation during inspiration caused by the weight of heavy abdominal viscera. Consequently, in equines the abdominal muscles are suggested to share the respiratory pumping tasks with the diaphragm by lifting the abdominal organs during expiration and thus overcoming the inertial and gravitational forces during tidal breathing. (Koterba et al 1988:344.) In horses, these physical features are most likely involved in adoption of biphasic breathing pattern during tidal breathing.

The abdominal fulcrum formed by the abdominal organs acts a reinforcer of the diaphragmatic contractive function and can be defined as a point of support for the diaphragm during inspiratory muscle action. This function assists the diaphragm in the expansion of the lower rib cage especially in a dog. (De Troyer et al 1984: 30; Decramer

et al 1984:1489). In a horse the different orientation of diaphragm and the heavy abdominal viscera cause the abdominal fulcrum to contribute less to diaphragmatic activation during inspiration.

5.3.2.3 Resting volume as a reflection of the physical equilibrium

The resting volume of the respiratory system can be defined as the point of physical equilibrium during respiration, where the forces from the outward recoil of the chest wall, and the inward recoil from lungs are counteracted. The resting volume is a state where respiratory muscles are passive. Thus, the outward recoil depends on the elastic characters of the rib cage, and the inward recoil depends on the viscoelastic properties of the lung, which are determined by the lung tissue properties and the alveolar tendency to collapse. The collapsing pressure results from the surface tension at the alveolar air-fluid interface. (as discussed earlier in chapter 5.1.2.3 Achieving the adequate alveolar ventilation with minimal cost) (De Troyer et al 1984: 30; Koterba et al 1988: 344; Frappell & MacFarlane 2005:144.)

In equine species the resting volume is greater than functional residual capacity which is different from majority of mammals. (Koterba et al 1988: 343). Consequently, the equine diaphragm is passively lengthened during the last part of expiration which is mechanically advantageous due to the storage of elastic energy. (Lafortuna & Saibene 1991: 256). Whereas in dog the resting volume and functional residual capacity are very close or equal. (Han, Gayan-Ramirez, Merigian & Decramer 1994:22). Therefore, the expiration in dogs occurs mostly passively consequent to the relaxation of the inspiratory muscles. Thus, the point of physical equilibrium of the respiratory system is different in equine and canine species during tidal breathing favoring the adoption of biphasic tidal breathing pattern in the equine species for its part.

6 Discussion

6.1 Summary of the findings

The purpose of this study was to form a synthesis about the species-related characteristics of the breathing patterns and neurological control mechanisms of the equine and canine diaphragm during tidal breathing for the osteopaths who treat equine and canine patients. Understanding the normal, healthy function of the respiratory system and characteristics of the breathing pattern is essential in order to recognize possible alterations of breathing pattern. Already in the early writings of osteopathy it has been stated that one of the principal duties of an osteopath is to recognize the normal function of diaphragm (as stated in chapter 2.6 Diaphragm in osteopathy) (Still 1899:124). Since the research related to animal osteopathy is still very limited in numbers, there is a great need for new studies not only about the manual techniques applied during osteopathic treatment but also about the anatomical and physiological rationale behind them. (Hausler et al 2021:143; Nevin et al 2020:6; Domingues et al 2022:196; Patterson 2006:593).

This study was conducted as a scoping review, and the selected articles were analyzed with thematic analysis. Key findings of the thematic analysis are summarized below according to the six main themes described earlier in detail in the results section (see chapter 5).

6.1.1 Metabolism as the main drive for the ventilation

First, the metabolism is the primary motor for gas exchange of an animal. The overall metabolism of an animal determines the need for ventilation (as stated in chapter 5.1.1.1). The basic metabolic functions include the water balance maintenance, heat control, vocalization and coordination with postural changes. These functions produce CO₂ as one of their metabolic byproducts. Consequently, the changes in CO₂ concentration of blood resulting from metabolic processes have a great influence on the breathing pattern of all mammals. (Del Negro, Funk & Feldman 2018:353; Mortola 2019:48.) Moreover, to keep the metabolic requirements of the breathing within the sustainable limits, it is important to achieve the blood gas homeostasis with minimal respiratory work (as stated in chapter 5.1.1.2). At rest, the minimal respiratory work is achieved by matching the physical properties of the respiratory system with the adopted tidal breathing pattern. (Del Negro, Funk & Feldman 2018: 353; Mortola 2019:

51.) Additionally, the neural glia cells within the central nervous system contribute to adoption of certain breathing pattern as a metabolic support for respiratory neurons (as reported in chapter 5.1.1.3). These cells participate in the maintenance of the homeostasis of the neural tissue within the brainstem. (Del Negro, Funk & Feldman 2018:360.)

6.1.2 Physical properties of the respiratory system set the circumstances for breathing

The physical properties of the respiratory system, such as the elastic characteristics of the lungs and chest wall, including the thorax, abdomen and diaphragm, contribute to the adoption of tidal breathing pattern by creating certain physical circumstances for the breathing. (as stated in chapter 5.1.2.1). Moreover, at the underlying dimension within the lungs, the airflow resistance is affected by the tone of the smooth muscles of the airways (as reported in chapter 5.1.2.2). In addition, the physical properties of the alveolae, especially at the air-fluid interface on their surface, also contribute to the adoption of certain tidal breathing pattern. (as described in chapter 5.1.2.3) (Frappell & MacFarlane 2005:146; Del Negro, Funk & Feldman 2018:356; Fisher & Sant'Ambrogio 1985:121; Coleridge & Coleridge 1989:3; Yu 2005:236.)

6.1.3 Typical parts of tidal breathing

Typically, the tidal breathing pattern in mammals always consists of inspiration, often postinspiration and sometimes active expiration in certain species, such as in equines (as stated in chapter 5.3.1.1). Therefore, it seems that the inspiratory muscle contraction is a key feature of mammalian breathing (as reported in chapter 5.1.3.1). The optional phase of postinspiration has been suggested to benefit the alveolar ventilation and to aid in smoother transition between inspiration and expiration. (as stated in chapter 5.1.3.2). Expiration may include active and/or passive components depending on the chosen tidal breathing pattern of an individual. The appearance of diaphragm during mammalian evolution may have contributed to the adoption of passive expiratory phase, which in turn may have increased the efficiency of breathing. (as described in chapter 5.1.3.3) (Del Negro, Funk & Feldman 2018:356; Koterba 1988:343, 344.)

6.1.4 The neural control of the tidal breathing

According to the findings of this study, the respiratory control of the diaphragm during tidal breathing is a multidimensional phenomenon consisting of some integral factors.

In general, the ventilation results from the conversion of the neural output to the respiratory movement by the lungs and chest wall, including thorax, abdomen and diaphragm. Remarkable differences in the neural control mechanisms between the equine and canine species were not found during this scoping review apart from the certain features of the motoric fibres of the phrenic nerve in canines. (as described in chapter 5.2.1.4) (Frappell & MacFarlane 2005:143; Mortola 2019: 52; De Troyer et al 1982: 36.)

At the level of the central nervous system several structures, such as the neural glia cells (e.g. astrocytes), central chemoreceptors, respiratory-related central pattern generators (CPGs) and inspiration related neural microcircuit, the preBötzinger Complex (preBötzc), are involved in the breathing-related processes during tidal breathing. (as stated in chapter 5.2.1.1) (Del Negro, Funk & Feldman 2018: 353; Coleridge & Coleridge 1989: 44.)

The important sensory role of the vagus nerve cannot be denied as an essential part of the neural control of breathing (as reported in chapter 5.2.1.2). The vagal respiratory-related sensorial fibres, the airway mechanoreceptors, (i.e. vagal afferents) have substantial significance in the maintenance of continuous breathing. The vagal afferents of the respiratory system include three main types of receptors: slowly adapting stretch receptors (SARs), rapidly adapting stretch receptors (RARs) and respiratory C-fibres. (Coleridge & Coleridge 1989: 11; Yu 2005: 218).

In addition, the peripheral arterial chemo- and baroreceptors influence greatly to the regulation of breathing. (as stated in chapter 5.2.1.3) These neural receptors perceive CO₂, O₂, pH- and pressure-related changes within the arterial blood at the branch between internal and external carotid arteries. Moreover, they participate in inhibition and excitation of breathing and the tone of the smooth muscles of the airways. (Coleridge & Coleridge 1989: 44,49; Del Negro, Funk & Feldman 2018: 353; Yu 2005: 236.)

Sensory and motor input from the phrenic nerve influence both the sensorial (i.e. afferent) integration at the level of the brainstem, and the muscular contraction of the diaphragm. (as described in chapter 5.2.1.4) (Coleridge & Coleridge 1989: 53.) Furthermore, the sensorial feedback from beyond the respiratory system, such as the proprioceptive input from the connective tissues of the chest wall also contributes to distribution of respiratory-related information within the brainstem. (Coleridge & Coleridge 1989:52; Mortola 2019: 49).

6.1.5 Tidal breathing patterns of equine and canine species

Tidal breathing pattern is a consequence of variable amounts of active and passive components during both inspiration and expiration depending on the individual. Adoption of certain tidal breathing pattern results from combining the physical traits determined by the anatomical characteristics of the individual, and the requirements from the external and internal environment of an animal. (Art & Lekeux 1988: 300; Mortola 2019:52.)

During tidal breathing in equine species, the first phase of inspiration seems to be primarily passive due to passive lung inflation after the relaxation of the respiratory-related abdominal muscles. The second phase of inspiration is active, and the diaphragm has a great role in it. During the first phase of the expiration, after the active phase of the inspiration, the passive deflation of the lungs occurs due to the relaxation of the inspiratory muscles. Subsequently, the second, active phase of the expiration is elicited by the contraction of abdominal muscles (as stated in chapter 5.3.1.1). (Koterba et al 1988: 343; Koterba et al 1995b: 266.)

Typically, the canine species adopt the monophasic breathing pattern during tidal breathing, which is defined as a breathing strategy where the inspiratory phase is active, and expiration occurs for the most part passively due to inward recoil of the lungs (as stated in chapter 5.1.2.3 and 5.3.1.2). This breathing pattern has economical advantages because it decreases the energy demand to needed to overcome the elastic resistance of the lungs and chest wall. (Del Negro, Funk & Feldman 2018: 351).

6.1.6 Species-related differences in the physical properties of the respiratory system

The main differences of the canine and equine breathing pattern during tidal breathing are related to the tissue qualities of the chest wall, to gravitational and inertial factors, and to the point of physical equilibrium, in which the two above mentioned properties participate. (Frappell & MacFarlane 2005:144; Han et al 1994:22).

Equine and canine species have certain distinct differences in the physical properties of their respiratory systems. Despite of the similar level of lung elasticity, the stiffness of the equine chest wall is greater compared to canines and many other terrestrial mammals. However, the stiff equine chest wall leads to increase of elastic work of breathing, which possibly results in adoption of the biphasic tidal breathing pattern to minimize the metabolic cost of the respiration. (Koterba et al 1988:344.) Whereas in canine species

more compliant chest wall results in active inspiration and passive expiration during tidal breathing (as stated in chapter 5.3.2.1).

Furthermore, the breathing-related gravitational and inertial forces are different in equines and canines (as described in chapter 5.3.2.2). Most likely, the different configuration of the equine diaphragm and the greater weight of the abdominal organs in comparison to canines contribute to adoption of biphasic tidal breathing pattern in equine species. Consequently, the abdominal muscles are suggested to share the respiratory pumping tasks with the diaphragm in equines by lifting the abdominal organs during expiration and thus overcoming the inertial and gravitational forces during tidal breathing. (De Troyer et al 1984: 30; Koterba et al 1988:344.) The abdominal fulcrum formed by the abdominal organs contributes to the expansion of the lower rib cage especially in a dog. (De Troyer et al 1984: 30; Decramer et al 1984:1489). In a horse the different orientation of diaphragm and the heavy abdominal viscera cause the abdominal fulcrum to contribute less to diaphragmatic activation during inspiration.

Moreover, the resting volume of the respiratory system can be defined as the point of physical equilibrium during respiration, where the forces from the outward recoil of the chest wall, and the inward recoil from lungs are counteracted. The resting volume is a state where respiratory muscles are passive. Thus, the outward recoil depends on the elastic characters of the rib cage, and the inward recoil depends on the viscoelastic properties of lungs, which are determined by the lung tissue properties and the alveolar tendency to collapse. (De Troyer et al 1984: 30; Koterba et al 1988: 344; Frappell & MacFarlane 2005:144.) In addition, in equine species the resting volume is greater than functional residual capacity which is different not only from canines but also from majority of other mammals. (Koterba et al 1988: 343). Consequently, the equine diaphragm is passively lengthened during the last part of expiration which is mechanically advantageous due to the storage of elastic energy. (Lafortuna & Saibene 1991: 256). Whereas in dog the resting volume and functional residual capacity are very close or equal. (Han et al 1994:22). According to the findings of this study these distinct differences in the physical properties of equine and canine respiratory systems are some of the key factors contributing to the typically different tidal breathing patterns in these animals.

6.2 Interpretations, possible explanations and potential implications

Even if often overlooked, the disruptions leading to disease can only be determined and eventually corrected to restore the healthy state if the normal bodily functions are

thoroughly understood. (Billman 2020:3) In the context of osteopathic treatment of animals, the assessment methods of normal, healthy tidal breathing pattern have not yet been established. The normal, diaphragmatic breathing pattern involves coordinated motion of the upper ribcage, lower ribcage and abdomen and requires adequate function of the diaphragm. (Sikora et al 2024:1). In humans, diaphragmatic breathing has suggested to influence on the function of autonomic nervous system by decreasing sympathetic activity and improving baroreflex sensitivity. (Yau & Loke 2021). Furthermore, it has been stated that diaphragmatic breathing may reduce blood pressure (both systolic and diastolic), produce greater cardiac blood volume and facilitate venous return from lower limbs. (Tsakona, Kitsatis, Apostolou, Papadopoulou & Hristara-Papadopoulou 2025:1).

Abnormalities of the normal, healthy breathing pattern are possibly related to various diseases and health complaints. In humans, the breathing pattern disorders, such as hyperventilation has been linked to various pathological conditions, such as cardiovascular and respiratory diseases. (Ok, Park & Park 2018:1). Additionally, abnormal breathing pattern has been linked to variety of musculoskeletal complaints. (Bradley & Esformes 2014: 29). Furthermore, it has been suggested that the breathing pattern abnormalities and inefficient use of the diaphragm might also be linked to cervical pain in humans. (Sagrillo & Frigo 2016: 414). Thus, the recognition of breathing pattern alterations could possibly improve the quality of osteopathic care offered to animal patients.

Benefits of deep, diaphragmatic breathing have been widely recognized in different populations, such as gastrointestinal cancer patients (Rezaei, Salari, Jasmi, Abdi & Shohaimi 2024: 7), in chronic obstructive pulmonary disease (Mendes, Moraes, Hoffman, Vieira, Ribeiro-Samora, Lage, Britto & Parreira 2019: 143) and in stress-related conditions both when measured with physiological biomarkers, and with self-reported questionnaires. (Hopper, Murray, Ferrara & Singleton 2019: 1865). Moreover, implementing of diaphragmatic breathing exercises has been shown to improve cognitive and mental functions and reduce stress related cortisol levels in healthy adults. (Ma, Yue, Gong, Zhang, Duan, Shi, Wei & Li 2017: 874). However, implementation of breathing exercises to animal patients is rather difficult due to lacking direct verbal communication. Thus, it would be interesting to study the possible short-term and long-term effects of osteopathic manual techniques on the adopted breathing pattern in animal patients.

With respect to above-mentioned, certain osteopathic techniques have been observed to improve one of the respiratory parameter values, peak of expiratory flow (PEF), with

statistical significance in humans. The authors of the study in question suggest that improvement of mechanical chest mobility and changes in overall tone of the autonomous nervous system resulting in airway relaxation and balanced muscle tone are the most probable factors contributing to the improvement of PEF values. (Stępnik, Kędra & Czaprowski 2020: 7.) However, similar research setting cannot be directly applied to animals receiving osteopathic manual treatment because of required forceful expiration on demand during PEF measurement. Nevertheless, possibly other respiratory measurements, such as spirometry could be implemented for animals during the same type of research setting. Burnheim et al (2016) have suggested that spirometry is a suitable, noninvasive technique to assess the respiratory function in horses, and moreover well tolerated by them.

Furthermore, it has been recently suggested that osteopathic manual treatment of upper cervical region may elicit parasympathetic changes and consequently affect vagal tone. (Cavanagh, Cope, Smith, Tolley, Orrock & Vaughan 2024: 452) As stated in chapter 5.2.1.2 (The sensory role of the vagus nerve), the afferent fibres of the vagus nerve within the respiratory system contribute significantly to the integration of breathing pattern. It has been suggested that alterations in respiratory rate and depth may both influence and be influenced by the autonomous nervous system resulting in alterations of breathing pattern. (Benjamin, Moran, Plews, Kilding, Barnett, Verhoeff & Bacon 2020: 282; Kirkman 2014: 540).

Still, despite of the promising conclusions, the efficacy of osteopathic treatment in regards of treating musculoskeletal complaints in humans is highly variable. (Esteves, Cerritelli, Kim & Friston 2022:4). However, Cerritelli, Chiacchiarretta, Gambi, Saggini, Perrucci & Ferretti (2021) have showed in their recent study that osteopathic manual treatment has a quantifiable effect by modifying the cerebral blood flow (CBF) at the level of central nervous system and peripheral level by altering the heart rate variability (HRV). Heart rate variability reflects autonomic nervous system's control on the heart which is constantly affected by respiration, blood pressure and central nervous system (via the central autonomic network). (Gullett, Zajkowska, Walsh, Harper & Mondelli 2023: 35). These findings are interesting from the perspective of the current study, since not only breathing influences the HRV, but also because of the state of autonomic nervous system contributes to regulation of breathing via the vagus nerve (as discussed earlier in chapter 5.2.1.2).

Moreover, HRV measurement devices suitable for animals exist and have been suggested to provide a useful tool in assessing the autonomic regulation of the cardiovascular system. (Fernandes & de Azevedo Cruz Seara 2021:15). During recent years the HRV measurements has been mostly used in veterinary behavioural research, but they could be applicable for assessment of the state of autonomic nervous system in other settings too. (Bidoli, Erhard & Döring 2022:2). Interestingly, it is widely recognized that the autonomic nervous system has a significant role in the homeostatic maintenance of an animal as well. (Malik, Hnatkova, Huikuri, Lombardi, Schmidt & Zabel 2019: 2596).

Notably, one of the essential aspects underlying the adoption of certain tidal breathing pattern is the organism's tendency to maintain homeostasis. (Mortola 2019:48). Already since 19th century, the physiologists have recognized the body's inherent tendency to maintain the internal stability which protects and buffers the organism against the constant changes of the external environment. The French physiologist, Claude Bernard (1813-1878), who has been regarded as the founder of modern physiology, has concluded that: "The stability of the internal environment is the condition for the free, independent life." (as translated from French by Billman 2020) (Billman 2020: 3.) Thus, deeper understanding about the breathing as one of the key elements in maintaining the homeostasis of the organism is of a great importance.

In their recent study, Somppi, Törnqvist, Koskela, Vehkaoja, Tiira, Väätäjä, Surakka, Vainio, Kujala (2022) investigated the effect of the relationship between the dog and their owner on the dog's emotional reactivity by measuring how the emotional situations influence on the dogs' physiological state according to HRV, and if the dogs' HRV, dogs' behaviour and the evaluations of the owner accompany each other in various situations. Even though the HRV measurements have been applied to welfare assessment of livestock since 1970s (Kovács, Jurkovich, Bakony, Szenci, Póti & Tózsér 2014:316), it has not yet been systematically applied to assess the autonomous nervous system's cardiac-related activity in equines and canines. This could provide valuable insights about the parasympathetic nervous activity of the animal, which is related to breathing via the vagal afferents. (Laborde, Allen, Borges, Dosseville, Hosang, Iskra, Mosley, Salvotti, Spolverato, Zammit & Favelle 2022).

The need to recognize and understand the normal, healthy characteristics of breathing have been argued already in this study. However, to understand the phenomenon of breathing and function of diaphragm even more extensively it could be interesting to

approach it from evolutionary perspective as well. Veit & Browning (2021) state concisely that "...One cannot understand organismal design without an understanding of various evolutionary tradeoffs organisms have been designed to solve."

Evolutionary veterinary medicine is a concept deriving from the Darwinian, or evolutionary medicine which is a field of study established by Nesse and Williams in 1991. (LeGrand & Brown 2002: 556). This approach implements the principles of evolutionary biology into veterinary medicine. Recently, evolutionary medicine applied on human patients and even wider populations, such as public health sector, has gained more recognition globally. (Natterson-Horowitz, Aktipis, Fox, Gluckman, Low, Mace, Read, Turner & Blumstein 2023:2). In their recent article, Place, Eddy & Bray (2023:1) have highlighted that osteopathy has many similarities and common interfaces with the evolutionary medicine. Both in evolutionary medicine and osteopathy the interaction between structure (anatomy) and function (physiology) is one of the elementary characteristics. (Place, Eddy & Bray 2023: 3). For instance, in the context of the current thesis, the elastic characteristics of the chest wall (i.e. anatomy) have direct influence on the adopted tidal breathing pattern (i.e. function).

In mammals the minor circumference of the alveolae and their small-scale radius of curvature create forces which makes their lungs relatively low in compliance in comparison for instance to reptiles and birds. This characteristic is counteracted partly by secretion of lung surfactant (as described in chapter 5.1.2.3). In addition, the evolutionary development of the diaphragm together with the musculature of rib cage has created highly efficient muscular suction pump to counteract above-mentioned features of the alveolae. It is astonishing to understand that without the development of the diaphragm during evolution lung function wouldn't be as effective as it is in mammals today. (Hsia, Schmitz, Lambertz, Perry & Maina 2013:894; Perry & Dunker 1980: 321.) Further studies about the the intra-thoracic and intra-abdominal pressure environment, and their interrelationship could give new insights about the maintenance and possible importance of breathing-related pressure dynamics both during activities and at rest.

Consequently, evolutionary perspective sheds light on the following observation as well, since the fundamental differences in respiratory-related physical characteristics include the differences in visceral mass, which in equines is large due to herbivore characteristics of this animal. Moreover, the respiratory-related gravitational and inertial forces are greater in equine species (as stated in chapter 5.3.2.2). Whereas canines, as predators, are not developed to eat constantly resulting in significantly shorter and less complex form of their digestive system. (De Cuyper, Meloro, Abraham, Müller,

Codron, Janssens & Clauss 2020: 1.) As Place, Eddy & Bray (2023:3) highlight, osteopathy has its roots in evolutionary thinking and therefore the osteopathic profession could benefit from conscious restoration of evolutionary perspective into the current osteopathic reasoning.

6.3 Limitations, ethical considerations and validity of scoping review

This scoping review had some limitations. Although thematic analysis offers a possibility to inductively extract new and deep insights from the analysed data, there are some challenges to this analysis method. Because thematic analysis is rather subjective as a method, the results of the study are prone to the bias of the author of the study. Such bias may include the preconceived ideas, prejudices or perspectives of the corresponding author. (Braun & Clarke 2006; Braun & Clarke 2019.) In this study the possible bias included the perspective of the author, especially during the theme generation.

However, during this study the whole process has been pursued to be described as openly as possible but certainly the author's limited experience from both scoping review process and thematic analysis have made an impression to the final result. At its best, in reflexive thematic analysis the researcher's engagement with the data includes continuous reflection and awareness of the researcher's role in theme generation. (Ayre & McCaffery 2021: 78).

Validity and transparency of the scoping reviews can be increased by involving several people to the reviewing process and critical appraisal of the included articles, and therefore team approach with more than one reviewer is considered as the best practice. (Lockwood, Borgess dos Santos & Pap 2019:292). However, only the author of this Master's thesis herself with very limited experience of conducting scoping reviews was involved in the whole process, which obviously may have affected to the results. On the other hand, the critical appraisal of the included articles was performed and the scores of the appraisal of each article are stated at the last column of Appendix 2. (The summary of data from selected articles including the quality assessment). There was some variety within the scores of critical appraisals of the selected articles. Based on the quality assessment, all of the narrative reviews (n=5) and one expert opinion were assessed as high-quality data. Whilst the quality assessment of the quasi-experimental studies (n=10) ranged from 4 out of 9 points to 8 out of 9 points. Hence, the scored points of the quasi-experimental studies had the mean value of 6,3 of 9 points. This may also be partly due to the wide range of date inclusion of the studies, since the more recent studies had higher scores from the critical appraisal. However, none of the

articles were omitted from the analysis after the critical appraisal. This was a conscious decision by the author of this study with the goal to acquire as broad view as possible to this relatively novel subject within the field of animal osteopathy.

Nevertheless, the author of this Master thesis reports no conflicts of interest in this work. Additionally, Turnitin plagiarism detection application (Turnitin 2025) has been used to confirm the authenticity of this work. Moreover, the guidelines of responsible conduct of research (RCR) established by Finnish National Board on Research Integrity TENK are followed throughout this master thesis. According to Finnish National Board on Research Integrity TENK (2023), good research practices include for instance carrying out the review in a transparent manner, respecting the rights of authors and establishing the overall quality of research including the study design, methodology and analysis of the results.

Several articles included in this scoping review were based on the scientific experiments performed on animals of different species. The ethical aspect of testing the scientific hypotheses on animals raises number of concerns. Simultaneously these experiments may produce valuable knowledge and understanding of the physiological functions of the animal species themselves, which may improve the veterinary care in critical situations (e.g. during emergencies or surgical operations requiring anaesthesia), but throughout the history many biomedical interventions performed on humans have been based on animal experiments. (Hajar 2011). The respect for animals and the concerns of their welfare are valid arguments to promote their health and wellbeing. According to Hajar (2011), the call for more humane treatment of animals has led to 3Rs campaign, which calls for 1) the replacement of animals with non-living models; 2) reduction in the use of animals; and 3) refinement of animal use practices.

Scoping review as a method of study did not require a research permit because no personal data was gathered during the process. Moreover, no external sources of funding were included either. During the search process, the preliminary search statement was refined with the help of librarian from Metropolia UAS, Sirja Pohjonen. However, search strategy was not peer reviewed by another librarian using the Peer Review of Electronic Search Strategies (PRESS) checklist, which is a recommended protocol in PRISMA Extension for Scoping Reviews (PRISMA-ScR) according to Tricco, Lillie, Zarin, O'Brien, Colquhoun, Levac, et al. (2018). The conduction critical appraisal is not mandatory in scoping reviews, but the assessment and reporting the risk of bias may be included by reviewers if desired. (Munn et al 2018: 6). However, in this master thesis included the use of PRISMA-ScR checklist to ensure the higher transparency and

credibility of the whole review process. Any external funding was not received for the completion of this study.

Despite of the certain above-mentioned limitations, this Master's thesis may provide valuable information to practising animal osteopaths, but also to the future generations of osteopaths who are willing to specialize in animal osteopathy. In addition, it is the sincere wish of the author of this thesis that this work succeeds in sparking the inspiration in anyone who finds the breathing phenomenon as fascinating as the author herself.

6.4 Future recommendations

According to the findings of this study, the anatomical proportions and physical characteristics of the lungs and chest wall of an animal plays a significant role in tidal breathing pattern adoption. For instance, the relatively stiff chest wall of the equines most likely participates significantly to the adoption of biphasic tidal breathing pattern. (Kotterba et al 1988). Consequently, it could be intriguing to study whether typical tidal breathing patterns exist in certain canine or equine breeds. Or are there certain differences of connective tissue type or body conformation which could predispose to alterations of tidal breathing pattern caused by altered biomechanics of breathing in either animals or humans? Moreover, could the certain kinds of tidal breathing patterns expose to breathing pattern disorders in animals or humans? Furthermore, from osteopathic perspective, does osteopathic manual treatment induce changes in the tidal breathing pattern, and if so what kind of? And from the evolutionary perspective, could it be that the horse as a prey animal has somehow benefitted from adoption of the biphasic breathing pattern during evolution?

In conclusion, experimental studies related the canine and equine breathing patterns in relation to the autonomic nervous system function in different situations would be beneficial to gain deeper insights of the whole phenomenon of breathing and the role of vagus nerve in health and disease. Possibly, this could be achieved by combining the HRV measurement with spirometry or other noninvasive methods to assess the respiratory function of animals in various settings. Furthermore, well-designed studies are needed to determine the possible breathing-related effects of osteopathic manual techniques on breathing both in animals and humans.

7 Conclusions

This endeavor of this thesis was to provide a synthesis about the characteristics of the equine and canine tidal breathing patterns and the neural control mechanisms of the diaphragm during tidal breathing not only for osteopaths treating equine and canine patients, and to professionals, such as veterinarians, animal physiotherapists and animal trainers, but also for the caretakers of animals who seek relief for their animal companions. Perceiving of the several overlapping dimensions of the tidal breathing pattern adoption and respiratory control in equines and canines may assist not only with understanding this phenomenon, but also with recognizing the possible alterations in it.

According to the results of this study, during tidal breathing, the metabolism functions as the primary motor behind the gas exchange of an animal, whilst the physical properties of the lungs and chest wall consisting of thorax, abdomen and diaphragm, set the circumstances for breathing. Breathing itself requires the conversion of the central and peripheral neural output to the respiratory movement by the lungs and chest wall (especially the diaphragm of a key importance), which have certain species-related differences in their physical properties. Finally, the cyclical alternation between the phases of inspiration, nonobligatory postinspiration and expiration results in the species-specific tidal breathing pattern of equines and canines with biphasic and monophasic characteristics, respectively.

It is noteworthy that wider recognition of the characteristics of healthy, normal tidal breathing patterns and multilayered neural control of the diaphragm in equines and canines within the profession of animal osteopaths could give valuable insights to the osteopathic manual treatment as well, since the breathing is foundational for life in all mammals.

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Appendix 1: Data search strategy

The preliminary search statement carried out in test searches on 24th March 2025:

1. (diaphragm AND equine OR canine (configuration OR anatomy OR anatomic* OR function OR function* OR neural control OR neural control* OR innervation) AND tidal breath* OR tidal breathing)

After refining as advised by the librarian carried out on 25th March 2025:

2. (diaphragm OR "respiratory muscles") AND (equine OR canine OR dog OR horse) AND ("tidal breath*" OR "mechanics of breathing")

The final search statement in ProQuest Central database after further addition of default, Anywhere except full text (NOFT), which is a choice specific to ProQuest Central database carried out on 26th March 2025:

3. (diaphragm OR "respiratory muscles") AND noft(equine OR canine OR dog OR horse) AND ("tidal breath*" OR "mechanics of breathing")

The final search statement in Science Direct and Wiley Online databases carried out on 28th and 30th March 2025:

4. (diaphragm OR "respiratory muscles") AND (equine OR canine OR dog OR horse) AND ("tidal breath*" OR "mechanics of breathing")

Detailed process of the data search is described below:

A preliminary search was carried out in ProQuest Central database in March 2025, using the following terms for the title, abstract and keywords (where applicable): (diaphragm AND equine OR canine (configuration OR anatomy OR anatomic* OR function OR function* OR neural control OR neural control* OR innervation) AND tidal breath* OR tidal breathing). After the preliminary search the keywords and index terms used in the initial findings were analyzed to refine the search strategy. The following step was a comprehensive search after refining the keywords and index terms in the ProQuest Central, Science Direct and Wiley Online Library databases. The third step of the study selection process included reviewing the reference lists of all selected studies to find any additional relevant sources. The search strategy was documented, and extracted data was charted in table form including the essential information about the data.

Before the discussion and advice from the librarian, potential key words were taken from the background articles' keywords and from possibly valid articles' keywords after the test search on 24th March 2025 with the initial search string (diaphragm AND equine OR canine (configuration OR anatomy OR anatomic* OR function OR function*

OR neural control OR neural control* OR innervation) AND tidal breath* OR tidal breathing). The following were the baseline keywords during the discussion: mechanics of breathing, respiratory mechanics, respiratory muscles and action of diaphragm.

The preliminary search was carried out in ProQuest Central on 25th March 2025 together with the librarian, Sirja Pohjonen. The original search string (diaphragm AND equine OR canine (configuration OR anatomy OR anatomic* OR function OR function* OR neural control OR neural control* OR innervation) AND tidal breath* OR tidal breathing) provided 30 082 results in ProQuest Central database when refined with the peer reviewed filter. With the help of librarian, the search string was refined to be as following: (diaphragm OR "respiratory muscles") AND (equine OR canine OR dog OR horse) AND ("tidal breath*" OR "mechanics of breathing"). This search provided 228 results.

Librarian's suggestion was to change the default of the search as Anywhere except full text (NOFT) which is a choice specific to ProQuest Central database, to better include the studies regarding to equine and canine populations to the search results. The following search string (diaphragm OR "respiratory muscles") AND noft(equine OR canine OR dog OR horse) AND ("tidal breath*" OR "mechanics of breathing") provided 20 results from which the majority was related to the research subject of this Master's thesis at the title level.

The first actual data search was carried out in ProQuest Central database on 26th March 2025. The applied search statement was following: (diaphragm OR "respiratory muscles") AND noft(equine OR canine OR dog OR horse) AND ("tidal breath*" OR "mechanics of breathing"). The search was refined by peer-reviewed filter and only results in English language was included. This search accomplished with 20 results.

The second data search was carried out in Science Direct database on 28th March 2025. The applied search statement was following: (diaphragm OR "respiratory muscles") AND (equine OR canine OR dog OR horse) AND ("tidal breath" OR "mechanics of breathing"). The default to search Anywhere except full text (NOFT) was taken off from the search string because it does not apply for Science Direct database searches. The search was refined by filters of review articles, research articles and English language. This search provided 244 results.

The third data search was carried out in Wiley Online Library database on 30th March 2025. The applied search statement was following: (diaphragm OR "respiratory muscles") AND (equine OR canine OR dog OR horse) AND ("tidal breath" OR "mechanics of breathing"). The default to search Anywhere except full text (NOFT) was taken off from the search string because it does not apply for Wiley Online Library database searches. The search was refined by filters journals and reference works (books were excluded) in English language. This search provided 84 results.

Altogether the database searches provided 348 results. The data was managed with Zotero software and exported to Rayyan (Rayyan QCRI application 2025) which is AI-powered Systematic Review Management Platform. The data was downloaded to Zotero software first and organized in three folders corresponding the database where the results were from. From Zotero the data was uploaded to Rayyan where the title, abstract and finally full text level screening was performed by the author of this thesis.

Appendix 2: The summary of data from selected articles including the quality assessment

Data charting table of selected articles applied from Hadie (2024:193) & Aromataris et al (2024:468)

Author/s, year of publication, title & country	Purpose/ objective(s) of the study	Methodological approach	Key findings	Quality assessment points
Art, T. and Lekeux, P. 1988. Respiratory air-flow patterns in ponies at rest and during exercise. Belgium.	To evaluate the changes in the equine breathing pattern caused by exercise by means of analyzing the configuration of respiratory flow-volume loops (TBVVL) during tidal breathing in ponies (n=10) both at rest and during standardized treadmill exercise.	Quasi-experimental study	During tidal breathing, the shape of the expiratory curves was biphasic in most of the ponies (n=8) and rather triangular in two ponies. Inspiratory flow patterns varied from monophasic and dome shaped (n=3) to biphasic (n=5) and triphasic (n=2) during tidal breathing. Despite of great variability between the ponies, each individual showed constancy in its own breathing pattern throughout the three daily investigations. The polyphasic breathing pattern of ponies at rest differs from that described for humans and dogs.	6/9 No ethical permission statement
Burnheim, K., Hughes, K.J., Evans, D.L. & Roldal, S.L. 2016, Reliability of breath by breath spirometry and	To characterize relative and absolute indices of respiratory function in healthy horses during tidal breathing (eupnoea) and carbon dioxide- induced hyperpnoea by using a	Quasi-experimental pilot study	During tidal breathing, all horses included in the current study demonstrated varying breathing patterns within the same day and on a breath-to-breath basis. Horses have significant respiratory reserve, and their ventilation can change rapidly in response to fear, excitement and other emotional changes. Therefore, some variability in tidal volumes and respiratory frequency was expected to occur. All horses included in the study	7/9 The study design was approved by

<p>relative flow-time indices for pulmonary function testing in horses. Australia.</p>	<p>modified mask pneumo-trachographic technique and to evaluate the reliability of this technique during three consecutive days.</p>		<p>demonstrated biphasic expiration during tidal breathing, but inspiration was monophasic, biphasic or both. In conclusion, the mask spirometry system used was able to produce reproducible and repeatable absolute and relative indices of respiratory function in healthy horses.</p>	<p>the Animal Care and Ethics Committee of Charles Sturt University</p>
<p>Coleridge, H., Coleridge, J. & Schultz, H. 1989. Afferent pathways involved in reflex regulation of airway smooth muscle. United States of America.</p>	<p>To describe the various sensory regions which are related to smooth muscles of airways, and the nature of sensory structures involved, including the intrinsic and extrinsic afferent inputs, located within the structures of the airways themselves and in the regions remote from airways and lungs.</p>	<p>Narrative review</p>	<p>The initiation of the breathing pattern is a consequence of various sensory inputs from both within the airways (intrinsic afferent input) and remotely from adjacent regions to airways and lungs (extrinsic afferent input). The motor activation of the smooth muscles of the airways results from sensory (afferent) feedback at various regions, including nasal and nasopharyngeal afferents; laryngeal afferents; reflexes from cold receptors; and lower respiratory afferents including vagal afferents, slowly adapting pulmonary stretch receptors, rapidly adapting receptors and both bronchial and pulmonary C-fibres.</p> <p>Lung volume also contributes to reflex responses of airways via various sensory receptors mentioned above. Naturally occurring autocooids (bradykinin, histamine and prostaglandins) also contribute into the sensory responses of the pulmonary and bronchial C-fibres. Both acute and chronic inflammatory response within the airways and lungs provokes sensory responses.</p>	<p>6/6</p>

			Extra-respiratory afferents inputs affecting the ventilation and bronchomotor tone are arterial chemoreceptors; arterial baroreceptors; cardiac afferents, including cardiac mechanoreceptors and cardiac chemosensitive afferents; afferents from skeletal muscle and diaphragm and afferents from digestive tract.	
De Troyer, A. <i>et al.</i> 1982. Action of costal and crural parts of the diaphragm on the rib cage in dog. Canada.	To explore the mechanism of the different actions of the costal and crural parts of the diaphragm on the rib cage in dogs by assessing the influence of lung volume, pleural pressure, abdominal pressure, the abdominal contents and the pericardial attachments of the diaphragm to the function of the costal and crural parts of the diaphragm. To investigate the segmental spinal innervation of the costal and crural parts of the diaphragm and the effect of the stimulation of the different roots of the phrenic nerve on the chest wall.	Quasi- experimental study	According to this study, costal and crural parts of the dog diaphragm have different action on the lower rib cage. The costal part appears to have a direct inspiratory action on the lower rib cage, whereas the crural part has an expiratory action on the lower rib cage when the abdomen is open. During the contraction of the crural part of the diaphragm, the consequent expiratory action is entirely due to the fall in pleural pressure occurring simultaneously. Most of the rib cage expansion during costal diaphragmatic contraction takes place mostly due to the fulcrum of the abdominal contents but also due to the increase in abdominal pressure. However, the pericardial ligaments of the diaphragm seem to play no role in the lower rib expansion induced by the costal part of the diaphragm. Phrenic nerve stimulation experiments showed that costal part of the diaphragm receives almost exclusively its motor innervation from the cranial segment (C ₅) of the phrenic nerve roots and the crural part from the caudal segment (C ₇) of the phrenic nerve in dog.	4/9 No ethical permission statement

Decramer, M. <i>et al.</i> 1984. Mechanical arrangement of costal and crural diaphragms in dogs. Canada & Belgium.	To determine the mechanical arrangement of the costal and crural diaphragms in dog by experimentally evaluating the separate behaviors of the two parts of the diaphragm during anesthesia.	Quasi- experimental study	Current study confirmed that the diaphragm in dog does not behave as a single entity expressing a uniform behavior. During tidal breathing, the crural part of the diaphragm usually shortened more and earlier than the costal part. The shortening of the crural part was frequently accompanied by the lengthening of the costal part during the early phase of inspiration.	4/9 No ethical permission statement
Del Negro, C.A., Funk, G.D. and Feldman, J.L. .2018. Breathing matters. United States of America & Canada.	To define the preBötzinger microcircuit, a medullary microcircuit which generates the rhythm of inspiration, and its interactions with additional breathing microcircuits, explore the mechanisms of rhythm generation and describe the effects of inspiratory breathing rhythm in relation to orofacial behaviors and possible effects on emotional regulation and cognitive function.	Narrative review	The rhythm of inspiratory muscle contraction, a defining characteristic for mammals, arises from the neural activity in the preBötzinger Complex (preBötzc). The expiration in mammals is usually passive during tidal breathing. However, the motor pattern of breathing in mammals often includes a third phase, postinspiration, occurring straight after the inspiration phase. Nevertheless, because the postinspiratory phase does not occur during anesthesia or sleep, it seems not to be essential for tidal breathing. There is a certain correlation with breathing pattern with the arousal state. Conclusively, the coupled neural oscillators including the interaction of the preBötzc with the conditional oscillators, are the main drive behind the inspiratory rhythm of intact mammals.	6/6
Fisher, J.T. and Sant'Ambrogio, G. 1985, Airway	To compare the physiological and morphological	Narrative review	During inspiration, the upper airway and respiratory pump muscles are recruited in coordination depending on vagally mediated, volume-related information from the mechanoreceptors	5/6

<p>and lung receptors and their reflex effects in the newborn. Canada & United States of America.</p>	<p>factors involved in respiratory pump and upper airway muscles of the newborn and adult. (Includes many experimental studies done for animals)</p>		<p>located in the airways and lungs. It is very likely that the postinspiratory muscle activity of diaphragm and other inspiratory muscles plays a significant role in newborns resisting the passive recoil of the respiratory system during the expiration phase. The newborn mammals are very likely to be obligatory nose breathers due to the lower nasal resistance compared to mouth resistance. The integrative processes related to breathing pattern of mammals are likely to be controlled mostly by central nervous system. After the birth the process of myelination of nerve fibers continues which explains the slower and less organized nerve conduction in newborn mammals. The superior laryngeal nerve provides mainly the sensory information from the upper airways. Bronchopulmonary C-fibers together with rapidly and slowly adapting mechanoreceptors (RAR and SAR), coursing with the afferent fibers within the vagus nerves, provide the sensory information from the lungs and airways.</p>	
<p>Frappell, P. B. & MacFarlane, P. M. 2005. Development of mechanics and pulmonary reflexes. Australia.</p>	<p>To provide an overview of the respiratory mechanics of the mammalian neonate at birth and during early development in combination with the action of vagal pulmonary reflexes which are required to establish and maintain the tidal breath-</p>	<p>Narrative review</p>	<p>The breathing pattern, ventilation and the resting volume of the lung are influenced by the mechanical properties and neuronal control of the respiratory system. In the newborn mammals, there is a tendency for alveoli to collapse and lung compliance (C_L) to decline, which is related to a high chest compliance/lung compliance (C_W/C_L) which promotes a low resting volume of the respiratory system (V_R) and decreased transpulmonary pressure.</p>	<p>6/6</p>

	ing and effective gas exchange during early development.			
Hall, L., Aziz, H., Groenendyk, J., Keates, H. & Rex, M. 1991. Electromyography of some respiratory muscles in the horse. Australia.	To investigate the activity of the costal part of diaphragm, intercostal, serratus ventralis, internal abdominal oblique, transversalis and rectus abdominis muscles in conscious horses and in the same horses when anesthetized. The serratus ventralis muscle tends to stabilize the chest wall in standing horse and possibly enlarges the diameter of the thoracic cavity during its contraction. The aim was to assess the possible contribution of the inactivity of serratus ventralis into the reduction of functional residual capacity with horses in recumbent position or during anesthesia. The possible contribution of other	Quasi-experimental study	In this study, the diaphragmatic inspiratory electromyographic (EMG) activity lagged the onset of inspiration and the activity of transversalis and internal abdominis muscles started while the expiration was still incomplete according to the tracing recorded by a stethograph arranged around the chest at the level of the 12 th to 13 th ribs. During tidal breathing, the abdominis transversalis muscle was found to be usually active during expiration in conscious horses. Minor contribution to the final part of expiration was recorded from the internal oblique muscle as well. The main finding was the high amplitude of tonic activity of the serratus ventralis during standing and absence of activity in anesthetized horses which corresponded to the hypothesis of the study.	6/9 This study design was approved by the University of Queensland Animal Experimentation Ethics Committee

	muscles usually considered as having a respiratory function was also determined.			
Han, J., Gayan-Ramirez, G., Megirian, D. & Decramer, M. 1994. Contribution of the parasternal intercostals to inspiratory rib elevation in dogs. Belgium.	To estimate the contribution of the parasternal intercostals to the elevation of the ribs during tidal breathing in anesthetized dogs. The relative contribution of the parasternal intercostal muscles to inspiration after diaphragm paralysis was assessed at the first experiment. At the second experiment, the mechanical interaction between different costal interspaces and several parasternal muscles was estimated.	Quasi-experimental study	During tidal breathing in intact animals, two phases of rib elevation were recorded in all dogs. The relaxation of the expiratory muscles and the activation of the parasternal muscles had a significant contribution to rib elevation during tidal breathing in anesthetized dogs. The mechanical interaction between parasternal intercostal muscles at each intercostal space is likely to be present but limited during tidal breathing.	7/9 No ethical permission statement
Koterba, A.M. <i>et al.</i> 1988 Breathing strategy of the adult horse (<i>Equus caballus</i>) at rest. United	To explore the mechanism underlying the polyphasic breathing pattern of the equine species by recording the tidal volume, airflow, rib cage and abdominal motion, and	Quasi-experimental study	During tidal breathing, the equine abdominal muscles appear to share the principal pumping duties with the diaphragm resulting in biphasic inspiratory and expiratory airflow pattern. The resting neuromuscular strategy of the horse, combined with relatively stiff chest wall, allows the horse to breathe	7/9

States of America.	the sequence of muscle activation including the diaphragm, intercostal, and abdominal muscles during tidal breathing. Additionally, abdominal, esophageal and transdiaphragmatic pressures were recorded with balloon-tipped catheters.		around the resting volume of the respiratory system which minimizes the total elastic work of breathing.	No ethical permission statement
Koterba, A.M., Wozniak, J.A. and Kosch, P.C. 1995 Ventilatory and timing parameters in normal horses at rest up to age one year. United States of America.	To report the changes in equine ventilatory and timing parameters during the first year of life to gain better understanding about both the changes in respiratory function related to growth and the breathing pattern of the adult horse.	Quasi-experimental study	Despite of significant decrease in respiratory frequency, the minute ventilation in the growing foal increased during the first year of life because of progressive rise in tidal volume. The young foal seems to use a breathing pattern with high frequency of breathing rather than large tidal volume in order to meet its relatively high ventilatory requirements probably due to the high metabolic rate during neonatal period. The results suggest that the lung growth in the horse is possibly dysanapctic, meaning that the increase in body size exceeds the lung growth in the maturing foal during the first year of life.	7/9 No ethical permission statement
Koterba, A.M., Wozniak, J.A. and Kosch, R.C. 1995 Changes in breathing pattern in the normal horse at rest up to age one year.	The purpose of this study was to report the transition in the breathing pattern of the horse from a monophasic to biphasic airflow pattern during the first year of life and to specifically evaluate the	Quasi-experimental study	The results suggest that the respiratory control mechanisms may play an essential role in the expression of the equine polyphasic breathing pattern. The timing of changes observed in airflow pattern and electromyographic (EMG) activation pattern of expiratory and inspiratory (abdominal, intercostal and diaphragm) muscles were considered to be temporally related. Inspiration in foals seemed to be an entirely active process	7/9 No ethical permission statement

United States of America.	influence of a stiffening chest wall on the breathing pattern of the equine species.		whereas in adult horse the passive component of inspiration was observed.	
Lafortuna, C.L. and Saibene, F. 1991 Mechanics of Breathing in Horses at Rest and During Exercise. Italy.	To study the respiratory mechanics together with the rate of work of breathing in five healthy adult Standardbred horses at rest and during different levels of exercise on a treadmill with incline of different degrees. The respiratory mechanics and the rate of mechanical work of breathing were also compared with those of other mammals of different size.	Quasi-experimental study	<p>According to this study, horses seem to be more economical breathers in comparison to human and dog. It seems that the diaphragm can store elastic energy by passively stretching during the last part of expiration in a horse during locomotion, which helps in overcoming the respiratory inertia during the beginning of inspiration. A great fraction of total respiratory work is contributed to the expiratory muscles which reduces the demand of inspiratory muscles in exercising horses.</p> <p>At rest, there is a significant linearity of the pressure/flow relationship displayed by the horse's respiratory system. The findings indicate that some degree of turbulence in airflow occurs in the respiratory system of a horse during tidal breathing. Consequently, it seems that horses have some mechanisms counteracting the increase in airflow and turbulence above the resting values and the tendency of the airways to collapse (the intrathoracic during expiration and the extrathoracic during inspiration).</p>	8/9 No ethical permission statement
Mortola, J. P. 2019. How to breathe? Respiratory mechanics and	To evaluate the aspects of respiratory mechanics and their possible influences into the breathing pattern newborns and adults. The aim was also	Narrative review	The coordination between lung mechanoreceptors, sensing absolute and tidal changes in lung volumes, and chest wall proprioceptors providing sensory information about the muscle length and force contribute to the optimal breathing pattern. The breathing pattern of mammals seems to be sensitive to changes in the mechanical properties, therefore being possibly	6/6

breathing pattern. Canada.	to assess the relationship between optimal breathing pattern and mechanical respiratory characteristic to gain better understanding of the most economical way of breathing. (Includes various findings about mammalian breathing strategies)		a poor indicator of changes in the central neural output. The broad conclusion of this study was that the breathing pattern producing the adequate alveolar ventilation (ml/min) with minimal cost, is the adopted breathing pattern adopted by newborn and adult mammals.	
Yu, J. 2005. Airway mechanosensors. United States of America.	To depict a model about airway mechanosensors and explain their characteristics mechanistically.	Expert opinion	Describes a comprehensive model of mechanosensory unit of airways including receptor classification, structure-function relation of the sensor, sensor behavior, encoding and decoding of the sensory information.	6/6

Appendix 3: The initial codes of the thematic analysis

Codes	Definitions
Resting volume reflects the physical equilibrium	<p>A point of physical equilibrium during respiration where forces from the outward recoil of the chest wall and the inward recoil from lungs are counteracted. The relaxation volume is a state where respiratory muscles are passive. Thus, the outward recoil depends on the elastic characters of the rib cage, and the inward recoil depends on the viscoelastic properties of the lung which are determined by the lung tissue properties and the alveolar tendency to collapse. The collapsing pressure results from the surface tension at the alveolar air-fluid interface.</p> <p>In horse the resting volume is greater than functional residual capacity which is different from majority of mammals.</p> <p>In dog the resting volume and functional residual capacity are very close or equal.</p>
Polyphasic tidal breathing pattern has varying components of active and passive phases	During the inspiration and/or expiration clear peaks in airflow and respiratory muscle activation are detected and consequently the breathing pattern is bi-, or triphasic depending on the number of detected peaks.

	<p>Biphasic tidal breathing pattern is the chosen breathing pattern in a healthy, adult horse.</p> <p>The demand of O₂ increases when fleeing a predator which results in increase of the active component of expiratory phase and expiratory muscle recruitment, and compulsion of the lungs below the relaxation volume follows. Thus, increase in ventilation is achieved if the breathing frequency does not decrease.</p>
<p>Monophasic tidal breathing pattern has economical advantages</p>	<p>During the inspiration and expiration no peaks of airflow or respiratory muscle activation are detected, therefore the airflow is monophasic during both inspiration and expiration. This tidal breathing pattern is chosen by foals under year of age and dogs, as well as the most of other terrestrial mammals.</p>
<p>Breathing pattern has a capacity to adapt to both long and short-term changes in the external environment and internal milieu.</p>	<p>The timing and pattern of each breath are controlled by Breuer- Hering reflexes which have their foundation on the feedback from the vagal afferent stretch receptors from the respiratory pump muscles and lungs.</p>

<p>Control mechanisms have their foundation on the interconnections between several neural structures</p>	<p>Genetics influence to the development and behavior of respiratory-related neurons as well, but their interpretation is beyond of the analytic knowledge of the author of this thesis.</p> <p>Inspiration, postinspiration and expiration are driven by three distinct, coupled oscillator in the brainstem. When all three phases are displayed, the preBötzC conducts the coordination of the phases.</p> <p>Medullar level: PreBötzinger Complex</p> <p>In the brainstem chemosensory neurons and glia cells react to changes in pH, O₂ and CO₂ levels in the cerebrospinal fluid and transmit the synapses to preBötzC and respiratory-related areas to maintain the homeostasis of an organism.</p> <p>Also, the peripheral chemo- and baroreceptors influence greatly to the regulation of breathing. Carotid sinus baroreceptors inhibit both the smooth muscle tone of the airways and breathing. Whereas carotid body chemoreceptors have an excitatory effect both on breathing and the airway smooth muscle tone.</p> <p>Interneurons act as a relay between the input from the stretch receptors of the lungs and inspiratory preBötzC. Consequently, the rhythmical inhibition of inspiratory preBötzC and excitation of</p>
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expiratory lateral parafacial nucleus (pF) related to initiation of expiration results in alternating inspiration and expiration.

Phrenic motoneurons

The phrenic sensory afferents from the diaphragm contribute to reducing the resistant work of breathing by evoking bronchodilatation. The physiological explanation for this phenomenon remains unclear but it most likely has a metabolic origin.

Airway mechanoreceptors, i.e. vagal afferents have substantial significance in the maintenance of continuous breathing. Vagal denervation results in irregularities of breathing rhythm, decreased lung compliance, apnea and even respiratory failure in newborns of various species. (Frappell & MacFarlane 2005:150). During tidal breathing, the changes in lung compliance and volume are perceived by the vagal afferent receptors which can induce reflexes which dynamically adjust the respiratory mechanics by causing alterations in the breathing pattern, tonic activity of respiratory muscles and the airway smooth muscle tone.

Slowly adapting stretch receptors (SARs) detecting static changes in lung mechanics have a great influence on the tidal breathing pattern in animals (appears to be less so in humans). The rhythmic discharge of SAR especially during the inspiratory phase of tidal breathing is the primary component of vagal afferent input from the lower respiratory tract.

Rapidly adapting receptors (RARs) detecting dynamic changes in lung mechanics have a minor importance during tidal breathing. RARs are activated more during larger changes in lung volumes, such as during rapid deflation but also often demonstrate higher activity during the peak of the inspiratory airflow. RARs may contribute significantly to Hering-Breuer deflation reflex which occur after rapid decrease in lung volume and consists of quick termination of expiration and following augmentation of inspiration. Although traditionally observed in newborns, the greater number of RARs found adult dog in comparison to puppies supports the existence of this reflex also in mature dogs.

SARs are greater in number than RARs, correspondingly 15% and 4% of the total airway receptors. Lung mechanoreceptors also have a great significance in postinspiratory phase together with pontine (located at the pons of the brainstem) circuits. Both SARs and RARs depend on the lung compliance to be stimulated, which can also be interpreted from their names related to stretch (of the lung tissue they are located in).

Nonmyelinated vagal afferent respiratory C-fibres also contribute in the mechanotransduction from the airways but respond changes in chemical stimuli (e.g. in case of inflammation or infection) rather than physical stimuli. These C-fibres may still contribute significantly to the regulation of tidal breathing by being related to smooth muscle tone of airways and the tonic activity of respiratory muscles. Their afferent input is interpreted and integrated with the breathing pattern generation at the level of brainstem.

	<p>Neural glia cells, such as astrocytes may contribute to the function of preBötzc as an inspiratory initiator by metabolically supporting the preBötzc neurons. The glial toxins have been shown to disturb the inspiratory rhythms in vitro studies. The regulation of the critical physiological variables, such as pH and O₂ are likely to be facilitated by astrocytes within the brainstem.</p>
<p>Inspiratory muscle contraction is a key feature of mammalian breathing</p>	<p>The phase of respiratory activity where the lungs are inflated, the peak of diaphragmatic muscle activity is recorded, the intra-abdominal pressure increases, and the intrathoracic pressure decreases. May include active and/or passive components depending on the chosen breathing pattern of an individual.</p> <p>The rhythm of inspiration has its origins at the medullar microcircuit, preBötzing Complex.</p> <p>The present view suggests that the inspiration is the inexorable phase of the breathing cycle, while postinspiration and expiration are dependent.</p>
<p>Postinspiration is often manifested in many mammals</p>	<p>This phase occurs immediately after inspiration and consists of shortening of the laryngeal adductor muscles resulting in increase of airway resistance, and extension of the contraction of the diaphragm, which hinders the lung deflation. Most likely the vagal afferent mechanoreceptors have a significant role in the regulation of both the regulation of the laryngeal adductor recruitment and the post-inspiratory activity of the muscles of inspiration.</p>

	<p>Postinspiratory phase profits the alveolar gas exchange by lengthening the amount of time that inspired air stays in the lungs and reduces the probability of airway collapse by promoting laminar expiratory airflow during expiration.</p> <p>Postinspiration is not obligatory part of the breathing cycle or essential for tidal breathing since it does not occur during sleep or anesthesia.</p> <p>However, post-inspiratory activity of diaphragm and other inspiratory muscles may also be capable of counteracting the passive inward recoil of the respiratory system.</p>
Expiration	The phase of respiratory activity where the lungs are deflated (not fully), the intra-abdominal pressure decreases, and the intra-abdominal pressure increases. May include active and/or passive components depending on the chosen breathing pattern of an individual.
The phases of inspiration, postinspiration and expiration alternate rhythmically during the breathing cycle	Simultaneous activation of inspiratory and expiratory muscles is not desirable during tidal breathing.
Active components of expiration are needed more to reach the functional	The lung volume at the end of normal, tidal expiration.

residual capacity (FRC) in a horse, in comparison to dog	<p>In horse the FRC is lower than relaxation volume during tidal breathing, whereas in dog both are approximate to each other.</p> <p>In dog at FRC the inspiratory force elicited by the rise of intra-abdominal pressure and the expiratory force elicited by the fall in pleural pressure cancel each other, which means that FRC and relaxation volume are equal in healthy individuals during tidal breathing.</p>
Elastic work component of the total work of breathing	The elastic work of breathing (and anatomical dead space) is kept within limits by background activity of vagal bronchomotor fibers resulting in adequate contraction of the smooth muscle of the airways.
Resistant work component of the total work of breathing	The phrenic sensory afferents from the diaphragm contribute to reducing the resistant work of breathing by evoking bronchodilatation, which results in reduction of flow resistance.
Peak airflow during inspiration or expiration reflects the timing and amount of active and passive components of the chosen tidal breathing pattern	<p>Individual variations of peak airflow (PF) results from the blueprint of the breathing pattern.</p> <p>Despite of the individual variability, it has been proposed that in healthy horses, the peak of expiratory airflow (PEF) typically occurs during early in expiration and peak of inspiratory airflow (PIF) late in inspiration.</p>

	<p>In the study of Burnheim et al (2016: 10) the expiratory flow after PEF in the studied horses typically had a biphasic pattern.</p>
<p>Physical properties of the respiratory system affect to the effectiveness of ventilation</p>	<p>The ventilation, breathing pattern and the relaxation volume of the lung are directly affected by the physical properties of the respiratory system.</p> <p>The stiffness of the equine chest wall contributes to adoption of biphasic tidal breathing pattern.</p> <p>The respiratory system including the lungs, airways and chest wall has its species- and age-related physical properties. More specifically, the chest wall consists of thorax, abdomen and diaphragm which are the structures that move during lung inflation and deflation. The ventilation results from the conversion of the neural output to the respiratory movement by the lungs and chest wall. The physical properties of these structures contribute significantly to the outcome of the whole breathing pattern phenomenon.</p> <p>Possibly the viscoelastic properties of the tissues are responsible for the receptor behavior. Thus, the dynamical or static changes of the mechanical properties of the respiratory system may also account for the changes in receptor sensitivity.</p>
<p>Metabolism as the primary motor for gas exchange</p>	<p>Primarily the most important factor in determining the need for ventilation is the overall metabolism of an organism which determines the adequate need for gas exchange.</p>

	<p>Delivering oxygen to the tissues is the common task of both respiratory and cardiovascular systems and therefore they are effectively coupled and coordinated.</p> <p>The changes in CO₂ levels have a great influence on the breathing because of its direct effect on the pH of an organism. However, the same is not the case with the change in the levels of O₂, which does not provoke immediate changes in the breathing pattern.</p> <p>The glial cells may be significant contributors to the maintenance of homeostasis of the neural tissue by participating in the metabolic processes within the brainstem. And thus, facilitating the proper function of the breathing CPG as the breathing pattern generators.</p>
Water balance maintenance, heat control, vocalization, coordination with postural changes and locomotion	Basic functions of an animal affecting to the adopted breathing pattern.
Ventilatory responses to different states	<p>Ventilation can become modified in response to fear and other emotional states both in a horse and in a dog.</p> <p>Arousal levels are unquestionably correlated with breathing pattern.</p> <p>The vagal bronchomotor tone is influenced by 'central state' (i.e. during REM sleep).</p>

	<p>The pattern of respiratory muscle activity is state-dependent.</p> <p>The emotions, such as relief, exhaustion, grief or happiness may provoke higher sighing frequencies during tidal breathing.</p> <p>Respectively, the preBötzC has also direct and indirect connections to other brain regions responsible of emotions, cognition and arousal and therefore the breathing pattern can influence these functions as well.</p>
Abdominal fulcrum as a reinforcer of the diaphragmatic contractive function	<p>A point of support for the diaphragm during inspiratory muscle action formed by the abdominal organs, which contributes to the expansion of the lower rib cage (especially in a dog).</p> <p>In a horse the different orientation of diaphragm and the heavy abdominal viscera cause the abdominal fulcrum to contribute less to diaphragmatic activation during inspiration.</p>
Intrathoracic pressure changes	The pressure within the thorax which changes during the phases of respiration.
Intra-abdominal pressure	Adequate rise in intra-abdominal pressure is required for the optimal function of the costal and crural parts of the diaphragm in a dog.

Transdiaphragmatic pressure in relation of diaphragmatic muscle action	Sufficient changes in the transdiaphragmatic pressure during tidal breathing reflect the ability of the diaphragm to generate force. Changes in transdiaphragmatic pressure are related to the muscle action of the costal and crural parts of the diaphragm
Zone of apposition	The area where the diaphragm is directly apposed to the inner surface of the lower ribcage. During inspiration the rise in intra-abdominal pressure contributes to the expansion of the lower rib cage via this zone.
Changes in lung volume	Contribute to the activation of the costal and crural diaphragm in dog during tidal breathing via the amount of force elicited through the zone of apposition.
Motor innervation differences for the costal and crural parts of the diaphragm	<p>Cranial segments (C₅) are related to the motor innervation of the costal part of the diaphragm and caudal segments (C₇) are related to the motor innervation of the crural part of the diaphragm in a dog.</p> <p>In horse the differences of segmental motor innervation of the parts of the diaphragm were not explored in the data set of the current scoping review.</p>
Lung compliance	The elastic characteristics of lungs. The compliance of both lungs and the chest wall measured during active respiration is lower than those under passive conditions.

	<p>During tidal breathing the lung compliance decreases because the small lung units tend to collapse due to the removal of surfactant from the inner surface of the alveolae and bronchioles. Decreased compliance during tidal breathing is reversed by the regular single deep breaths, or sighs.</p> <p>The breathing pattern is altered during sudden changes in lung compliance because the SARs within the airways become activated.</p>
Chest wall compliance	<p>The elastic characteristics of the thorax, abdomen and diaphragm.</p> <p>The decrease of chest wall compliance during development contributes to passive maintenance of FRC by increasing the stiffness of the chest wall and therefore having greater resistance to the inward recoil of the lungs.</p>
Individual blueprint of breathing pattern	<p>The breathing pattern is a consequence of variable amounts of active and passive components during both inspiration and expiration depending on the individual.</p>
Airway smooth muscle tone	<p>Results from the central chemoreceptors at the level of the medulla reacting to e.g arterial CO₂ levels, and the efferent (bronchomotor) tone of the vagal branches and affects to the breathing pattern.</p>

	<p>Has an effect not only to dynamic lung compliance but also to airflow resistance. (Resulting in increase of resistant workload?)</p> <p>Also, the effects from bronchoconstrictor and bronchodilator reflexes influence the basal tone of airway smooth muscles.</p> <p>Sensory areas remote to the respiratory tract may also contribute to bronchomotor reflexes, such as arterial chemo- and baroreceptors, and from sensory nerve endings in the gut, skin, heart and skeletal muscles.</p> <p>The ventilatory dead space is decreased and airflow resistance increased when the smooth muscles are contracted.</p>
The initiation of the breathing cycle	<p>The inspiration-related rhythm is generated at the ventrolateral medulla, precisely the microcircuit of neurons called preBötzinger Complex (preBötzc).</p> <p>Several of the neurons' axons originating at preBötzc are related to the inspiratory rhythm generation, but numerous axons have direct connections to other brain regions as well.</p>

	<p>The axons of inspiratory-related neurons cross the midline resulting in bilateral synchronization at medullar level, but some of them also project towards the motor neurons that steer the muscles of inspiratory pump.</p>
<p>Regular sighs belong to breathing pattern during tidal breathing</p>	<p>Alveolae, as fluid-lined structures have high surface tension which needs to be exceeded by very high inspiratory pressure. The alveolae have a tendency to collapse at the end of each the expiration during tidal breathing. The low transpulmonary pressure combined with low lung volume increase the alveolar collapsing tendency.</p> <p>Regular sighs are required to reinflate the collapsed alveolae, to restore the surfactant to the surface biofilm of the alveolae and to prevent atelectasis during tidal breathing.</p> <p>Consequently, these larger inspiratory efforts belong to the normal breathing pattern. Sighs may occur in higher frequency in young mammals or during hypoxia when the atelectasis have higher tendency to occur due to increased breathing frequency.</p> <p>RARs are suggested to contribute into the generation of sighs due to increase in their activity when lung compliance is reduced during deflation of the lungs.</p>