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Review

From Science to Practice: A Review of Laterality Research on Ungulate Livestock

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Abstract: In functional laterality research, most ungulate livestock species have until recently been mainly overlooked. However, there are many scientific and practical benefits of studying laterality in ungulate livestock. As social, precocial and domestic species, they may offer insight into the mechanisms involved in the ontogeny and phylogeny of functional laterality and help to better understand the role of laterality in animal welfare. Until now, most studies on ungulate livestock have focused on motor laterality, but interest in other lateralized functions, e.g., cognition and emotions, is growing. Increasingly more studies are also focused on associations with age, sex, personality, health, stress, production and performance. Although the full potential of research on laterality in ungulate livestock is not yet exploited, findings have already shed new light on central issues in cognitive and emotional processing and laid the basis for potentially useful applications in future practice, e.g., stress reduction during human-animal interactions and improved assessments of health, production and welfare. Future research would benefit from further integration of basic laterality methodology (e.g., testing for individual preferences) and applied ethological approaches (e.g., established emotionality tests), which would not only improve our understanding of functional laterality but also benefit the assessment of animal welfare.

Keywords: hemispheric asymmetries; farm animals; emotional processing; animal cognition; development; human-animal interactions; animal welfare

1. Introduction

Research on functional hemispheric asymmetries, also referred to as functional laterality (from here on referred to as laterality), has benefitted from findings in non-human animals over several decades. Such findings have contributed to a better understanding of lateralized processing, especially with regard to its evolution [1,2]. As a result, it is now assumed that laterality first evolved on an individual level (individuals perform a certain task either with left or right hemispheric dominance) to benefit brain efficiency and second on a population level (the majority of individuals perform a certain task with hemispheric dominance in the same direction) to benefit social coordination [3,4]. Our understanding of laterality has specifically benefitted from knowledge gained from a few animal models, such as zebra fish, primates, chicks and pigeons [5]. For instance, research on primate hand preferences for different manual tasks has helped to better understand the evolution of human handedness [6]. Also, findings that exposure to light during different stages of incubation has crucial effects on the development of laterality in visual processing in chicks [7,8] has advanced our knowledge concerning the development of lateralization [9]. However, although these animal models provide much insight into laterality, it is important to remember that they reflect only a small proportion of the animal kingdom. Thus, to avoid a skewed overview of laterality, it is important to also study other groups of animal species. While for most wild animal species there may be practical limitations to studying their laterality, this is less of an issue for domestic species. Amongst domestic species, ungulate livestock have until recently been largely overlooked, despite their ready availability. A possible exception is horses, where many studies have investigated lateralized locomotion with regard to performance in sport [10]. In fact, most research on ungulate livestock has traditionally always had a more applied focus, being mainly dominated by research on production [11]. However, particularly in the study of farm animal welfare, it is increasingly acknowledged that insight from other disciplines (e.g., neurobiology, psychology, and pathology) is essential [12]. As a consequence, studies on emotions and cognition in ungulate livestock are now established research fields. Along these lines, such a development would also be expected for functional laterality (as an important aspect of emotional and cognitive processing). Nevertheless, it is only in the last two decades that functional laterality in ungulate livestock has slowly started to attract attention (Figure 1).

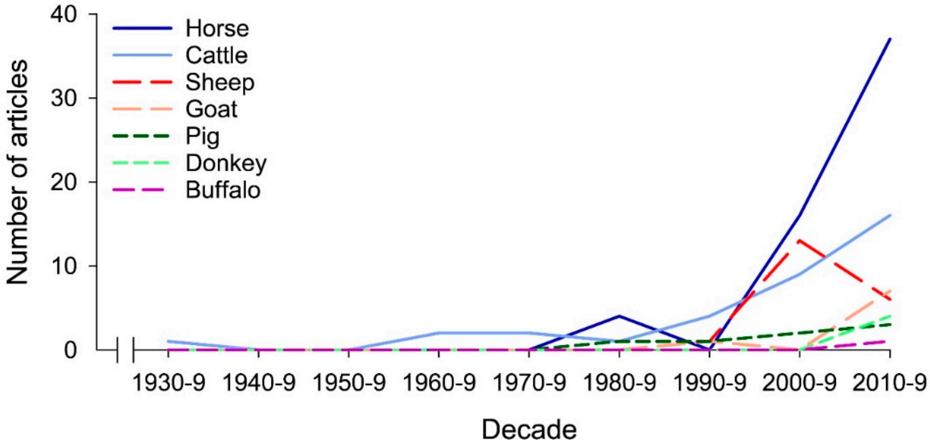

Figure 1. Number of peer-reviewed journal articles (in English) published per decade on laterality per ungulate livestock species. Articles were either collected using Web of Science, by scanning references in the obtained literature, or already in my possession (for details see Section 2).

Therefore, the aim of this review is to highlight the importance of studying laterality in ungulate livestock. First, the potential of research on ungulate livestock to increase knowledge on brain laterality will be discussed (Section 3). Second, in order to understand to which extent this potential is already exploited, an overview will be provided of the knowledge already obtained from laterality research on ungulate livestock (Section 4). Finally, some recommendations are provided for future research (Section 5).

2. Approach

For this review, research articles were considered that addressed functional laterality in ungulate livestock. Since there may be some disagreement concerning which species should be considered ungulate livestock, ungulate species were selected from the list of farm animals of the Food and Agriculture Organization of the United Nations [13]. Accordingly, the following species were considered: buffaloes, camelids, cattle, donkeys, goats, horses, mules, pigs and sheep. Since this review focuses on livestock, only (originally) domesticated species of each group were included, which means, for instance, that research on Przewalski horses [14,15] was excluded, but research on feral horses was included. Research articles from peer-reviewed journals that were written in English were searched using Web of Science (search terms: buffalo/camel*/cattle/donkey/goat/horse/mule/domestic pig/sheep + laterali*; last search: June 2019) and by scanning references in the obtained literature. These articles were added to publications that were already in my possession prior to this literature research. Articles that addressed laterality in behavior or brain activity were included if they had no major asymmetries in the setup (e.g., if the subjects were all trained to take the right-sided detour in a maze first [16]), if left and right sides were separately measured and if analyses of laterality on the individual and/or group level were reported. As a consequence, studies focusing only on asymmetrical behavior without a clear focus on its direction were excluded.

3. Why Study Functional Laterality in Ungulate Livestock?

Ungulate livestock as animal models in laterality research offer many opportunities that are either already exploited in current studies or could be exploited in future studies. First of all, as mentioned in the introduction, it is important to study laterality across a diverse range of species to better understand the different mechanisms involved in functional laterality and to better understand its evolution. Ungulate livestock represent different families in the ungulate clade and, as such, show considerable differences in morphology, physiology, ecology and behavior from the more commonly studied primates, fish and birds. One particularly valuable feature of many ungulates is that they have a, compared to many other mammals, relatively small binocular visual field [17,18] and high degree of decussation in their optical fibres, e.g., horses: 90% [19], cattle: 82.9%, sheep: 88.9%, pigs: 87.8% [20] (note that these features are also found in most birds and many other vertebrate species). Laterally placed eyes make it easier to reliably measure eye preferences, since it is easier to exclude possible input to the other eye. In addition, the high degree of decussation of optical fibres ensures that input from the used eye is predominantly processed in the contra-lateral hemisphere. As a result, ungulate livestock make excellent models for studying lateralized processes that involve the visual modality. Since ungulates have hooves instead of hands or paws and do not seem to have a wide array of facial expressions [21], they have evolved different motor functions for manipulation and the expression of emotions compared with primates and humans. For instance, the pig snout seems to fulfil similar functions as the hands of primates [22,23], with the essential difference that it is an unpaired organ [22], requiring a completely different type of manipulation and therefore possibly a different manifestation of laterality. Another example is the expression of emotions through ear and tail postures (e.g., [21,24–27]). The behavioral ecology of ungulate livestock also provides interesting opportunities for laterality research. For instance, as social mammals they are useful to study the incidence of population level laterality for functions with different levels of social coordination. Ungulate livestock species are also precocial, which means that brain development mainly takes place before birth, while in altricial species, such as rodents, this happens more after birth [28,29]. As a consequence, research on laterality in ungulates could provide new insights into the development of functional laterality [30]. In addition, studying functional laterality in ungulate livestock offers the chance to study the involved evolutionary mechanisms, as it would allow insight into potential changes in functional laterality during the process of domestication. Domestication is briefly defined as a process by which animals adapt to humans and to the captive environment [31]. It is accompanied by changes in morphology, physiology and behavior [32] and, therefore, could be expected to also affect behavioral laterality. Adaptation to humans especially may offer good opportunities to study laterality in inter-species communication, similar to what has been described for dogs, which have been reported to show lateralized processing of communicative [33] and emotional components [34] of human speech. Some studies on ungulate livestock species have already shown that these species are sensitive to human signals [35–37]. However, it may be expected that variation in the intensity and type of interactions with humans between different domestic species would also affect their appraisal of human signals. As a result, studying different domestic species with different domestication paths would allow better insight in the effect of adaptation to humans on lateralized processing. Ungulate livestock are also good models for studying the role of laterality in emotional processing and in the existence of individually distinct emotional reactivity patterns (also referred to as personality), because emotions and personality have usually been well studied in these species [38–40]. Therefore, there already is much knowledge about the expression of emotions in these species and good methodological approaches to study emotions and personality have already been developed, making it easier to study the role of laterality therein. There is also a growing body of studies on physical and social cognition in ungulate livestock [41], providing opportunities to study the role of laterality in cognitive performance. In addition, several of these ungulate species have been shown to be useful neuroscience models, such as pigs for modelling human brain disorders [42] and sheep for face identity and emotion processing [43]. Finally, one of the main reasons for studying laterality in ungulate livestock is for their own sake. Studying functional laterality has been suggested to provide insight into the underlying cerebral processes of emotions and expression of personality and, as such, benefit the study of animal welfare [44–46]. Furthermore, determining behavioral laterality may also aid in the assessment of stress and health risks [46–48]. Altogether, these considerations show that studying laterality in ungulate livestock entails considerable opportunities for advancing knowledge in the fields of neuroscience, cognitive sciences and animal welfare.

4. Insight Gained from Laterality Research on Ungulate Livestock

The search in Web of Science rendered 391 articles, of which 82 fulfilled the requirements presented in Section 2. A further 44 articles were found by scanning the references in the obtained literature. Combined with 6 publications that were already in my possession prior to this literature research and that did not turn up in either search method, this resulted in a total of 132 articles included in this review. Most research has so far been focused on horses and cattle (57 and 35 articles respectively; see also Figure 1), whereby it must be noted that most research on cattle has mainly focused on side preferences while lying and for entering the milking parlor, without referring to brain lateralization. There has been less research on sheep, goats, pigs and donkeys (20, 8, 7 and 4 articles, respectively), while there is only one study on laterality in buffaloes and no studies yet on camelids and mules. Most research was focused on observations of laterality in motor functions. Lateralized motor functions were sometimes studied to gain insights into the prevalence of motor laterality on an individual and population level (Table 1), but often also to study interactions between an individuals' hemispheric dominance and other individually distinct aspects, e.g., sex, age, personality, health and performance. Sensory modalities (visual, auditory, olfactory and touch), as well direct measures of brain activity, provided more insight into cognitive and emotional processing. A full overview on brain and/or behavioral laterality research in ungulate livestock is provided in Table 2. In this section, the findings will be discussed according to the significance of these findings for different scientific fields and practical applications.

Table 1. Overview of studies that reported statistical findings with regard to laterality in motor functions at a population or individual level. Only studies that reported the outcome of tests of significance at the group level are included (or, in rare cases, if all subjects showed the same pattern). Different outcomes for different subgroups/conditions are reported if statistics for the whole sample were missing.

	Directional Biases		**Individual Biases**	
	Significant	**Non-Significant**	**Significant**	**Non-Significant**
Horse	Locomotion: [49–53], [54] [1] Standing: [55,56], [57] [3], [58] [4] Stepping down: [59] Loading on truck: [59]	Locomotion: [58–66], [54] [2] Standing: [67], [57] [5], [58] [6] Stepping up: [59] Unloading from truck: [59] Obstacle avoidance: [64] Rolling: [64] Stretching: [55] Turning during flight: [68] Suckling: [69] Competition maneuvers: [70]	Locomotion: [53,61,63,64] Standing: [56] Obstacle avoidance: [64] Rolling: [64]	
Cattle	Lying: [71], [72] [7], [73] [8], [74] [9]	Lying: [75–80], [72] [10], [73] [11], [74] [12] Parlor entry: [78,81–83] Feeding: [78] Rumination: [78] Locomotion: [78] Tail swishing: [78] Side of track: [78]	Parlor entry: [78] [13], [81] [14] Lying: [78] [13] Feeding: [78] [13] Rumination: [78] [13]	Parlor entry: [78] [15], [81] [14] Lying: [78] [15] Feeding: [78] [15] Rumination: [78] [15] Locomotion: [78] Tail swishing: [78] Side of track: [78]

Table 1. *Cont.*

	Directional Biases		Individual Biases	
	Significant	**Non-Significant**	**Significant**	**Non-Significant**
Sheep	Obstacle avoidance: [84] [16], [85] [17] Foot movements during transport: [86] Side preference in maze: [87]	Obstacle avoidance: [84] [18], [85] [19] Stepping up: [84] Rumination: [84] Locomotion: [88] Lying: [88] Tail posture: [88]	Obstacle avoidance: [85] Side preference in maze: [89]	
Goat	Side preference in maze: [89]	Stepping down: [90]	Side preference in maze: [89]	Detour direction: [91] Stepping down: [90]
Pig	Lying during nursing: [92] [20] Tail posture: [22]	Lying during nursing: [92] [21] Manipulation with snout: [22]	Lying during nursing: [92] [22] Tail posture: [22] Manipulation with snout: [22]	Lying during nursing: [92] [23] Stepping up: [22] Stepping down: [22]
Donkey	Standing: [93] [24]	Standing: [93] [25]	Standing: [93] [24]	

[1] 18-month-old trained horses, [2] horses that were 8 or 12 months old or untrained, [3] racing breeds, [4] ridden horses, [5] working breeds, [6] unridden horses, [7] infected with *Mannheimia haemolytica*, [8] in the morning, [9] cows with mastitis, [10] not infected with *Mannheimia haemolytica*, [11] in the afternoon, [12] cows without mastitis, [13] intensively housed herd, [14] some months, [15] extensively housed herd, [16] ewes & 2-6 month old lambs, [17] ewes, [18] 4–6 days old lambs, [19] lambs, [20] 28 days after birth, [21] 7 & 11–12 days after birth, [22] 11–12 days after birth, [23] 7 & 28 days after birth, [24] large space, [25] small space.

Table 2. Overview of studies on functional laterality in ungulate livestock organized by species. Information included: total sample size (N), functional modality and a general description of the function, whether or not the study is included in Table 1 (T1; N = no, Y = yes) and which other aspects of laterality were studied: C = cognition, E = emotion (emotional responses within test), S = sex, A = age, Pe = personality (behavior in other tests), H = health/stress = Pr = production/performance, and outcome: - = not tested/reported, N = laterality/association not found, Y: laterality/association found.

Article	N	Modality	Function	T1	C	E	S	A	Pe	H	Pr
Horse											
[62]	10	Motor	Stepping pattern during trot	Y	-	-	-	-	-	-	-
[94]	30	Motor	Sidedness while being ridden	N	-	-	-	-	-	-	Y
[50]	4	Motor	Leading limb during gallop	Y	-	-	-	-	-	-	-
[54]	10	Motor	Stepping pattern during trot	Y	-	-	-	Y	-	-	-
[66]	30	Motor	Asymmetrical locomotion on a treadmill	Y	-	-	-	-	-	-	-
[55]	106 & 157	Motor & Olfactory	1. Forelimb while grazing 2. Hind leg stretching 3. Sniffing stallion feces	Y	-	-	N	Y	N	-	N
[64]	40	Motor/Visual	1. Forelimb while starting locomotion 2. Obstacle avoidance 3. Obstacle avoidance when ridden 4. Rolling direction	Y	-	-	Y	-	-	-	-
[57]	186	Motor	Forelimb while grazing	Y	-	-	-	Y	-	-	-
[95]	36	Touch	Mechanical nociception	N	-	-	-	-	-	N	-
[96]	65	Visual/Olfactory	Eye/nostril use while inspecting a novel object	N	-	Y	N	Y	-	-	-
[97]	24	Motor	Forelimb while grazing	N	-	-	-	-	-	Y	Y
[68]	30	Visual & Motor	1. Response to novel object from the side 2. Turning during flight	Y	-	Y	N	-	-	-	-
[53]	9362	Motor	1. Forelimb while starting to gallop 2. Forelimb at the start of a race 3. Stride pattern during gallop	Y	-	-	N	-	-	-	-
[98]	38	Visual/Olfactory	Eye/nostril use while inspecting objects	N	-	Y	-	-	-	-	-

Table 2. *Cont.*

Article	N	Modality	Function	T1	C	E	S	A	Pe	H	Pr
[99]	25	Touch	Mechanical nociception	N	-	-	-	-	-	N	-
[63]	219	Motor	Sidedness while being ridden	Y	-	-	Y	-	-	-	-
[58]	30	Motor	1. Cantering direction 2. Forelimb while grazing	Y	-	-	-	-	-	-	-
[100]	12	Auditory	Ear and head orientation towards conspecific whinnies	N	Y	-	-	-	-	-	-
[49]	9	Motor	Hoof's center of pressure during walking	Y	-	-	-	-	-	-	-
[101]	4	Motor	Asymmetrical changes in thoracic shape during locomotion	N	-	-	-	-	-	-	-
[102]	55	Visual/Motor	Entrance in arena with/without a human in the middle	N	Y	-	N	-	-	-	-
[65]	5	Motor	Forelimb loading during locomotion	Y	-	-	-	-	-	-	-
[103]	17	Motor	Forelimb while: 1. Grazing 2. Starting canter 3. Jumping	N	-	-	-	-	-	Y	Y
[56]	6	Motor	Leg movements during grazing	Y	-	-	-	-	-	-	-
[104]	10	Motor/Visual	Detouring a symmetrical/ asymmetrical barrier	N	-	-	-	-	-	-	-
[105]	28	Touch/Visual	Emotional reactivity to humans after unilateral tactile stimulation	N	-	Y	-	-	-	Y	-
[106]	6	Motor	Hoof's center of pressure on left and right circles	N	-	-	-	-	-	-	-
[107]	45	Visual/Touch	Response to approaching human from the side	N	-	Y	-	Y	-	-	-
[67]	24–66	Visual & Motor	1. Eye use during agonistic interactions 2. Head turn bias during vigilance and reactivity 3. Forelimb while grazing	Y	-	Y	N	Y	-	-	-
[108]	14	Motor/Visual	Side preference in Y maze	N	-	-	-	N	-	-	-
[109]	11	Motor	Body lean angle during turning	N	-	-	-	-	-	-	-
[110]	72	Visual/Auditory	1. Cross-modal discrimination between owner and stranger 2. Cross-modal recognition of familiar humans 3. Eye use to view humans 4. Head turn response to human voices	N	Y	-	-	-	-	-	-
[111]	46	Motor	Derailment during locomotion in a circle	N	-	-	N	Y	-	-	-
[69]	79	Visual/Motor	Suckling side	Y	-	N	N	Y	-	-	-
[51]	7	Motor	Hoof balance during locomotion	Y	-	-	-	-	-	-	-
[52]	11	Motor	Asymmetrical locomotion in a circle	Y	-	-	-	-	-	Y	-
[112]	20	Motor	Body lean angle during turning	N	-	-	-	-	-	-	-
[59]	14	Motor	Forelimb while: 1. Starting locomotion 2. Stepping up 3. Stepping down 4. Loading on truck 5. Unloading from truck	Y	-	Y	N	N	-	-	-
[113]	24	Touch	Response to pressure on side of body	N	-	-	-	-	-	-	Y
[60]	26	Motor	Asymmetrical locomotion	Y	-	-	-	-	-	-	-
[114]	12	Olfactory	Nostril use while smelling different odors	N	-	Y	N	-	-	-	-
[70]	482	Motor	Maneuvers during competition	Y	-	-	-	-	-	-	-
[115]	12	Motor	Leading limb during galloping	N	-	-	-	-	-	N	-
[116]	19	Visual/Motor	Turning during flight	N	-	N	N	N	-	-	-

Table 2. *Cont.*

Article	N	Modality	Function	T1	C	E	S	A	Pe	H	Pr
[117]	28	Visual	Eye use while viewing pictures of human faces	N	-	Y	-	-	-	-	-
[118]	6	Visual/Touch	Side of handler during trotting	N	-	-	-	-	-	-	Y
[119]	26	Motor/visual	Detouring a symmetrical/asymmetrical barrier	N	Y	-	-	-	Y	-	-
[120]	7	Motor	Asymmetrical locomotion	N	-	-	-	-	-	-	-
[61]	2095	Motor	Forelimb while starting to gallop	Y	-	-	Y	N	-	-	N
[121]	31	Visual	Eye use during affiliative behaviors	N	-	Y	-	-	N	-	-
[122]	8–27 pairs	Visual	Lateral preferences of mother-infant pairs during: 1. Slow travelling 2. Resting 3. Approach to suckle without detour 3. Approach to suckle with detour 4. Fleeing	N	Y	Y	N	N	-	-	-
[123]	17	Motor & Visual/Olfactory/Auditory	1. Relaxed forelimb position 2. Forelimb while starting locomotion 3. Forelimb while investigating box 4. Eye/nostril/ear use while inspecting novel object	N	-	-	-	-	Y	-	-
[124]	12	Visual/Brain activity	Attention to laser light	N	Y	-	-	-	-	-	-
[125]	28	Auditory	Ear movements while hearing human emotional vocalizations	N	Y	Y	-	-	-	-	-
[126]	46	Brain activity	Eye temperature after novel handling test	N	-	-	-	-	N	-	-
[127]	16	Visual & Motor	1. Eye use while approaching a novel feeder 2. Forelimb while grazing	N	-	-	-	-	N	-	-
[128]	96	Visual/Touch	Side of trainer while learning new task	N	Y	-	-	-	-	-	Y
Cattle											
[129]	~70	Motor	Lying side preference	N	-	-	-	-	-	-	-
[130]	73	Motor	Lying side preference	N	-	-	-	-	-	Y	-
[80]	388	Motor	Lying side preference	Y	-	-	-	-	-	-	-
[73]	35	Motor	Lying side preference	Y	-	-	-	-	-	-	-
[131]	217	Motor	Side in milking parlor	N	-	-	-	-	-	-	-
[132]	77	Motor	Lying side preference	N	-	-	-	Y	-	-	Y
[71]	6	Motor	Lying side preference	Y	-	-	-	-	-	-	-
[75]	44	Motor	Lying side preference	Y	-	-	-	-	-	-	Y
[81]	89	Motor	Side in milking parlor	Y	-	-	-	N	Y	Y	Y
[133]	108	Motor	Lying side preference	N	-	-	-	-	-	-	-
[83]	60–90	Motor	Side in milking parlor	Y	-	-	-	-	-	N	N
[78]	182	Motor	1. Tongue protrusion direction [feeding] 2. Jaw movement direction [rumination] 3. Forelimb while starting locomotion 4. Lying side preference 5. Tail swishing direction 6. Side of track 7. Side in milking parlor	Y	-	-	-	-	-	Y	-
[134]	24	Motor	Side in milking parlor	N	-	-	-	-	Y	-	-
[135]	max. 400	Visual	Arrival of food from the side	N	-	-	-	Y	-	-	Y
[136]	227	Motor	Lying side preference	N	-	-	-	-	-	Y	-
[137]	94	Motor/Visual	Obstacle avoidance	N	-	-	-	-	Y	-	-

Table 2. *Cont.*

Article	N	Modality	Function	T1	C	E	S	A	Pe	H	Pr
[138]	146	Motor	Side in milking parlor	N	-	-	-	-	-	-	-
[77]	248–250	Motor	Lying side preference	Y	-	-	-	N	-	-	Y
[79]	186	Motor	Lying side preference	Y	-	-	-	-	-	-	Y
[139]	12	Motor	Lying side preference	N	-	-	-	-	-	-	-
[140]	124	Visual	Eye use to observe an approaching human	N	-	Y	-	N	-	-	-
[141]	38	Motor	Lying side preference	N	-	-	-	-	-	Y	-
[142]	~1290	Motor	Lying side preference	N	-	-	-	N	-	N	-
[143]	40	Motor	Lying side preference	N	-	-	-	-	-	-	-
[144]	233	Visual/Motor	1. Eye use in agonistic interactions 2. Passing a familiar/unfamiliar person 3. Side while walking through a track	N	Y	Y	-	Y	Y	-	Y
[145]	78	Motor	Lying side preference	N	-	-	-	-	-	N	Y
[146]	~98	Motor	Lying side preference	N	-	-	-	-	-	-	Y
[147]	41	Motor	Lying side preference	N	-	-	-	Y	-	-	Y
[76]	195	Motor	Lying side preference	Y	-	-	-	N	-	N	-
[74]	12	Motor	Lying side preference	Y	-	-	-	-	-	Y	-
[148]	216	Visual/Olfactory	1. Observing bilaterally placed novel objects 2. Nostril use for sniffing novel objects	N	-	Y	-	-	-	N	-
[82]	72	Motor	Side in milking parlor	Y	-	-	-	-	Y	-	Y
[149]	202	Visual/Motor	1. Passing a novel person in a laneway 2. Side in milking parlor 3. Hanging tail	N	Y	Y	-	-	Y	-	Y
[72]	24	Motor	Lying side preference	Y	-	-	-	-	-	Y	Y
[150]	~4900	Visual	Response to approach of familiar looking/ masked human from the side	N	Y	Y	-	-	-	-	-
Sheep											
[89]	8	Motor	Side preference in T-maze	Y	-	-	-	-	-	-	-
[151]	20	Visual/Brain activity	Discrimination of sheep vs. human faces	N	Y	-	-	-	-	-	-
[152]	10	Visual	Effect of eye on face recognition	N	Y		-	-	-	-	-
[153]	10	Visual	Effect of eye use on human face recognition	N	N	-	-	-	-	-	-
[154]	6	Visual/Brain activity	Face recognition	N	Y	-	-	-	-	-	-
[155]	20	Visual/Brain activity	Viewing pictures of faces	N	-	Y	-	-	-	-	-
[156]	32	Motor	Side preference in T-maze	N	-	-	Y	-	-	Y	-
[88]	54	Motor	1. Forelimb while starting locomotion 2. Tail movement direction during suckling 3. Lying side preference	Y	-	-	N	-	-	-	-
[157]	57	Motor	1. Rotation around own axis 2. Obstacle avoidance 3. Forelimb in front of obstacle	N	-	-	-	-	-	Y	-
[84]	77	Visual & Motor	1. Obstacle avoidance to join flock mate/mother 2. Forelimb while stepping up 3. Jaw movement direction [rumination]	Y	-	Y	N	Y	-	-	-
[158]	3	Visual/Brain activity	Face recognition learning	N	Y	-	-	-	-	-	-
[159]	87	Motor	Side preference in T-maze	N	-	-	Y	Y	-	Y	-

Table 2. *Cont.*

Article	N	Modality	Function	T1	C	E	S	A	Pe	H	Pr
[21]	19	Motor	Ear postures	N	-	Y	-	-	-	-	-
[160]	34	Motor/Visual	Side of entrance in arena with novel & familiar objects	N	-	-	Y	-	-	Y	-
[161]	57	Visual & Motor	1. Obstacle avoidance to join flock mate/mother 2. Forelimb while stepping up 3. Jaw movement direction [rumination]	N	-	-	-	-	-	Y	-
[162]	27	Motor/Visual	Side of entrance in Y-maze with novel & familiar objects	N	-	-	-	N	-	Y	-
[87]	309	Motor	Side preference in T-maze	Y	-	-	-	N	-	-	N
[85]	86	Visual/Motor	Obstacle avoidance to join flock mate/mother	Y	-	Y	N	Y	Y	-	-
[86]	4	Motor & Visual	Steps during sea motion	Y	-	Y	-	-	-	Y	-
[163]	33	Visual/Motor	Eye use and ear postures while viewing videos of dogs and sheep	N	-	N	-	-	-	-	-
Goat											
[89]	11	Motor	Side preference in T-maze	Y	-	-	-	-	-	-	-
[164]	29	Visual & Motor	1. Effect of side of maze during maze learning 2. Forelimb while starting locomotion	N	Y	-	-	-	-	-	-
[165]	8	Brain activity	Brain activity during food expectation fulfilment and frustration	N	-	Y	-	-	-	-	-
[91]	42	Motor/Visual	Detour to access food	Y	-	-	-	-	-	-	-
[166]	7	Brain activity	Brain activity during resting	N	Y	Y	-	-	-	-	-
[90]	30	Motor	Forelimb while stepping down	Y	-	-	N	N	-	-	-
[167]	20	Motor/Visual	Side to access food inside transparent cylinder	N	-	-	-	-	N	-	-
[168]	18	Auditory	Head turn to conspecfic/heterospecific calls	N	N	N	-	-	-	-	-
Domestic pig											
[169]	5	Motor	Lying during nursing	N	-	-	-	-	-	-	-
[170]	32	Brain activity	Brain morphology after tethering	N	-	-	-	-	-	Y	-
[92]	11	Motor	Lying during nursing	Y	-	-	-	-	-	-	-
[171]	11	Brain activity	Brain morphology after tethering	N	-	-	-	-	-	Y	-
[22]	76	Motor	1. Side of snout used to open a flap door 2. Tail curling direction 3. Forelimb while stepping up 4. Forelimb while stepping down	Y	-	-	-	-	-	-	-
[172]	104	Visual	Eye use in agonistic interactions	N	-	N	Y	-	-	Y	-
[173]	76	Motor	1. Side of snout used to open a flap door 2. Tail curling direction	N	-	-	-	-	Y	-	-
Donkey											
[93]	19	Motor	Forelimb while standing	Y	-	-	Y	Y	-	Y	-
[174]	16	Touch	Mechanical nociception	N	-	-	-	-	-	N	-
[175]	16	Touch	Thermal nociception	N	-	-	-	-	-	N	-
[176]	36	Touch	Response to tactile stimulation	N	-	-	-	-	-	N	-
Buffalo											
[177]	112	Motor	Side in milking parlor	N	-	-	-	-	-	-	-

4.1. Motor Laterality

Human handedness shows a clear pattern, with approximately 90% of the human population preferring to use the right hand across many tasks [178]. In non-human vertebrates, laterality in motor functioning is often not found on a population level and may be more task dependent [3,6,179]. However, most of these studies have focused on hand or paw preferences. Insight from other expressions of sidedness in motor behavior could help to better understand the prerequisites for evolving laterality on an individual and population level. An overview of the findings for motor laterality on a population and individual level is provided in Table 1. The first striking information from this overview is the multitude of motor organs and functions that are studied. Although many studies on motor laterality could not be included because they reported no statistical outcome at the group level, the overview still provides some insight into motor laterality for different motor functions. It seems that the majority of the studies found no population level laterality, and many also found no individual level laterality, which may be explained by the seemingly low complexity of most of the studied functions [180]. Indeed, the variety of motor functions studied per species would allow testing to examine the effects of task complexity and to determine whether more complex tasks elicit stronger lateral biases [180]. One study in pigs partially supports this hypothesis, since manipulation with the snout elicited stronger individual biases than foot use for stepping up or down [22]. However, the same study also found that tail curling direction had even stronger individual, as well as population level, biases. Tail curling in itself is a seemingly simple motor function, but since tail posture may have some social function [181,182], this may account for the population level right bias. Similarly, sheep showed a right population bias for avoiding an obstacle while viewing a flock mate or mother, but no population biases for stepping up or ruminating [84]. Together, these findings support the idea that social coordination is an important driving force for the evolution of population level laterality [3] and that population level motor laterality may be determined more by the nature of the tasks than their complexity [183]. Several motor laterality studies on horses have shown how humans may influence the expression of motor laterality in domestic species, for instance, through breeding and training [54,57,58,94]. For example, horses that were trained or ridden showed population level biases in locomotion and standing, while unridden and untrained horses had no population bias [54,58]. However, other reports have suggested that training reduces laterality in locomotion [94], and since untrained horses are usually younger, age may also have played a role (see Section 4.4). Other studies reported that racing horse breeds showed a left forelimb preference at the population level, while a breed of working horses and feral horses did not [55,57,61]. These findings suggest that lateralized behavior may be triggered by close interactions with humans, which sheds light on possible effects of domestication on behavioral lateralization. Further research is required to clarify whether the human influence more likely increases or decreases lateralized behavior and to determine whether such effects are accompanied by changes in hemispheric dominance or are merely copying human behavior. Altogether, findings from ungulate livestock have helped to better understand the prerequisites for motor laterality at the individual and population level by shedding light on the effects of task complexity, social coordination and interactions with humans.

4.2. Cognitive Performance and Strategies

In humans, the two hemispheres are dominant in the processing of different types of cognitive tasks, e.g., the left hemisphere is specialized in processing language, and the right hemisphere is specialized in spatial processing and social recognition [184]. As a precursor for human language, conspecific vocalizations have been found to be processed with left hemispheric dominance in several species (reviewed in [185]). However, such studies are still rare, and findings from auditory laterality experiments in goats [168] and horses [100,125] do not provide support for this pattern. Therefore, more research is needed to better understand the auditory processing of conspecific vocalizations.

In contrast, in social recognition, there seems to be a consistent pattern across vertebrates, in which the right hemisphere is dominant for individual recognition and the left hemisphere dominant for category-based distinctions, e.g., between conspecifics and heterospecifics [186]. In this field, large amounts of new insights have been provided by studies on ungulate livestock, especially in sheep. In sheep, the recognition of conspecific faces is found to be mainly under the control of the right hemisphere [151,152,154,158], with sheep showing increased discrimination accuracy when pictures of familiar faces are presented in the left hemifield [152] and altered neural activity patterns (e.g., faster response latencies), suggesting a greater involvement of the right hemisphere during face recognition [151,154,158]. These findings show many similarities with human face recognition processing and therefore show that asymmetrical processing of sophisticated social cognition skills is not unique to humans [187]. Although sheep also learned to discriminate familiar and unfamiliar humans' faces, they did not show the same right hemispheric advantage, suggesting a lack of expert processing mechanisms in human face recognition [153]. An experiment on horses, in contrast, did provide evidence of lateralized processing during the recognition of familiar and unfamiliar humans [110], although in this case, the evidence pointed to left hemispheric dominance. The authors argued that although the right hemisphere may be responsible for initial recognition and responses to novelty, the left hemisphere may be responsible for the top-down retrieval of memories associated with specific individuals. This finding is to some extent supported by findings in which horses showed a right ear preference (indicating a left hemispheric advantage) when listening to the whinnies of neighbor horses (but not to strangers and group members; [100]). In contrast, foals were found to prefer to keep their mother in their left visual field [122]. Other findings for the responses of cattle and horses to humans provide conflicting results, with evidence supporting more right hemispheric involvement while viewing either familiar [102,150] or unfamiliar humans [144,149]. These differences may in part be due to differences in experimental set ups and varying degrees of familiarity with the humans. Thus, although the findings in ungulate livestock cannot provide a clear pattern yet, they do support the notion that both hemispheres may be involved in social recognition [110,186].

While in humans spatial cognition is found to be generally dominated by the right hemisphere [188], findings in non-human primates, birds and other animal species rather suggest that both hemispheres are involved in visual and spatial cognitive processing [189–191]. In ungulate livestock there are so far only a few indications of lateralized spatial cognitive processing. For instance, Baragli and colleagues discovered that strong lateral biases in horses (as shown by a persistence of individual side preferences to pass a barrier despite increasing asymmetry) may be part of a faster, but less flexible, strategy in solving a spatial task [119]. In another study, goats were found to learn a maze task faster when they were trained to use the left alley to exit the maze, which suggests a left visual field (and therefore right hemisphere) advantage for learning [164]. Further evidence for an important role of the right hemisphere in learning comes from findings that the right hemisphere guides attention processes [124,166]. Also, foals that kept their mother in their left visual field had fewer spatial separations from their mother, which suggested that they maintained spatial proximity better due to a right hemisphere advantage in visuospatial processing [122]. Altogether, these findings suggest an important role of the right hemisphere in spatial processing and learning, by which these findings could help to improve our understanding of spatial cognition across vertebrates. However, more systematic studies on spatial cognition in ungulate livestock are needed to gain better insight.

4.3. Emotional Processing

In a recent review on emotional lateralization in non-human vertebrates (44), it was concluded that the majority of evidence suggests left hemispheric dominance in food-related contexts and right hemispheric dominance in fear and aggression. Since food-related contexts may be more associated with positive emotions, while fear and aggression may be more associated with negative emotions, the majority of the evidence seems to support the emotional valence hypothesis, which suggests that negative emotions are processed with right hemispheric dominance and positive emotions with left hemispheric dominance (e.g., [192]). Findings from domestic species were concluded to be in accordance with the general pattern [44]. Indeed, the general pattern found in ungulate livestock in the present review still seems to support the emotional valence hypothesis, at least with regard to fear, since vigilance or responses in novel and/ or fear inducing contexts were often found to be directed by the left eye/ ear or right nostril ([59,67,68,86,96,98,107,114,117,140,144,149,150,166], but see [105,148] for contradictory findings). In contrast, right hemispheric dominance for aggression was only supported by findings in horses [67], while studies on agonistic behavior in cattle and pigs failed to find a bias at the population level [144,172]. Of the 3 studies that considered responses to food rewards [21,114,165], two supported the general pattern [21,165] and additionally suggested right hemispheric dominance during frustration when an expected food did not come [21]. Horses, unlike dogs [193], did not show a left nostril preference for smelling food [114], but a left nostril preference was associated with food-related behaviors such as licking and chewing. In the last review [44], there was insufficient evidence on sex and positive social contexts to draw any clear conclusions. Fortunately, more evidence has been gathered for these contexts since then, most of which seem to point to right hemispheric dominance [84,85,114,121,122,155]. For instance, a significant majority of horses showed a left eye bias during grooming and other mutual affiliative behaviors [121]. In contrast, horses have been found to show a preference to hold their right ear forward/ left ear backward when attending to human laughter [125]. Even though humans are not conspecifics, horses are in frequent contact with humans, so laughter may have positive emotional relevance for horses [27]. Finally, several other studies have failed to find any lateralized emotional processing [69,116,163,168]. Thus, lateralized emotional processing needs to be further studied in ungulate livestock to better understand emotional processing, but new findings in positive social interactions already provide a good start, since they have the potential to challenge the emotional valence hypothesis.

4.4. Development of Laterality and Sex Differences

In humans and other altricial species, the expression of laterality is not stable throughout the lifespan: functional laterality is slowly established during infancy [9] and has been found to decrease in older age [194]. Of the reviewed studies on ungulates, 29 examined the effects of age, of which 16 reported a significant effect (Table 2). Most of these effects concerned differences between juvenile and adult subjects. For instance, there are several reports on increased laterality with increasing maturation in horses [54,55,57,69,96,111]. However, in some of these findings, training may also have played a role (see Section 4.1), especially considering that feral horses show an opposite pattern with juveniles having stronger side preferences [67]. In sheep, it was reported that neonatal lambs had stronger individual biases than ewes [84]. However, in the same study (as well as in a later study [85]), ewes showed a population bias to avoid an obstacle to return to their flock, while lambs only showed individual biases to return to their mother. The effect of maturation on laterality in ungulate livestock therefore seems to be more complex and requires further study. Some studies in adult cattle have reported increased right laterality during lying in older cattle [132,147] and an increased preference for using the right eye in fights [144]. These findings are in contrast to findings in primates, where laterality was found to decrease in older age [194] and thereby provide interesting new insights into how laterality changes throughout the lifespan. Some studies also provide interesting insights in factors affecting the development of laterality. For instance, it has been reported that prenatal undernutrition in sheep shifts motor side preferences to the left [156] or to ambilaterality [159], which supports other findings that environmental factors during prenatal development alter the expression of laterality [9,195].

In humans and non-human mammals, there are some indications that males may be more right hemispheric dominant and females more left hemispheric dominant [196,197]. While several hypotheses have been put forward to explain these sex differences (e.g., that this results from different prenatal testosterone levels [198]), none of these is supported by sufficient evidence [197]. Although the effects of sex have been reported in 24 studies, only 8 of these actually found effects (Table 2). For instance, female horses were found to be right-biased in several motor functions, while males were left-biased in the same functions [63,64], and female pigs viewed their opponent more with the right eye during aggressive displays, while males more often used the left eye in this context [172]. These findings are therefore in line with the general trend in mammals. However, most studies failed to find any sex differences. Although these results may in part be due to small sample sizes, they still question the magnitude of such an effect. For both development and sex differences, however, it is clear that the full potential offered by research on laterality in ungulate livestock, especially considering the regular availability of newborns, has not been fully exploited, since many studies that included different sexes and age groups either did not analyze the effects of age and sex or did not report the outcome of these analyses.

4.5. Personality

As discussed in Section 4.1, individuals differ in their tendency to use one hemisphere more than the other, and due to the different involvement of these hemispheres in cerebral processing (Sections 4.2 and 4.3), this could lead to differences in the response to environmental stimuli [199]. Such responses are expressed through consistent coping styles or temperaments [183], also referred to as personality. While in humans there is no clear consensus on the association between handedness and personality [200], studies on non-human mammals often suggest that left-biased individuals are more fearful/less bold, more pessimistic and less explorative than right-biased individuals [183,201–203]. Some findings on ungulate livestock support this general pattern [149,173]. For instance, cattle that preferred to pass a novel human on the right (using the left eye to view the person) fled faster after physical restraint in a crush test [149], and pigs that were right-biased across two motor functions (snout use and tail curling) showed a shorter latency to touch a novel object compared with left-biased pigs [173]. They also interacted more often with this novel object, suggesting that they were also more explorative and vocalized more in isolation, which may be indicative of sociability [173]. However, other studies rather found an interaction between boldness and the strength of laterality [81,85,134]. For instance, ewes and lambs that showed strong laterality during an obstacle avoidance test spent more time close to a separating fence during a separation test [85], which the authors interpreted as the result of increased disturbance. This result is in line with findings that cows with consistent side preferences in the milking parlor have higher heart rates during udder preparation [81] and stood more motionless in a novel arena [134]. Three studies also provide insight into the coping style, with right-biased individuals showing a more proactive coping style (more active responses to restraint) than left-biased individuals ([82,144,173], although for pigs these results had low power [173]). This result seems to support Rogers' suggestion that the left hemisphere controls proactive behavior, while the right hemisphere controls reactive behavior [183]. In addition, several other findings in ungulate livestock suggest interactions with aggression [134], activity [134], dominance [134,144], cognitive bias [123] and behavioral flexibility [119], all of which may be argued to reflect certain aspects of individually consistent behavior. However, more research is needed to better understand the association between personality and laterality, and studies on ungulates could considerably contribute to a better understanding by incorporating observations of laterality in easy-observable motor functions (e.g., forelimb, ear or tail postures) in studies using already established emotionality tests [37,38].

4.6. Health, Stress and Welfare

In humans, laterality is often associated with various psychiatric and neurological disorders, including Parkinson's disease [204], schizophrenia [205], depression [206] and autism spectrum disorders [207], and several studies have shown a differential involvement of the hemispheres in immune responses [208]. While research on laterality in ungulate livestock is still far from providing any insight on human diseases, some studies have reported interactions with immune function. For instance, strong and weak lateralized ewes were found to differ in their immune responses to separation from their lamb [157], and strongly lateralized ewes were found to have higher metabolic rates during pregnancy [161]. In addition, other health issues were associated with altered expression of laterality. For instance, lameness was found to induce asymmetrical locomotion in horses only when they were circling to the left [52], which may indicate a higher sensitivity in the left legs. However, other studies in horses and cattle found no interaction between lameness and lateralized behavior [76,115,142,145,148]. In contrast, mastitis was found to affect lying side preferences of cows, with one study indicating a more left-sided preference [136] and another study indicating stronger side preferences (141). Bovine respiratory disease was also found to affect lying preferences, although the findings are contradictory, with one study indicating a switch to the left [72] and another study a switch to the right [74] compared to healthy controls. Significant forelimb preference while standing was associated with unevenness in hooves in young horses, which increases the risk of injury [97,103]. In contrast, in pigs a strong side bias during fighting was associated with shorter fights (although not with fight outcome; [172]), which means that strong laterality could also help to reduce the risks of injuries during fighting. The side of the body was, however, not found to affect sensitivity to tactile stimulation and nociception in horses [95,99] and donkeys [174–176]. Altogether these results show no clear pattern yet. Nevertheless, they illustrate that lateralized behavior can be associated with diseases and other health risks and can eventually be used as an indicator of such health risks.

Laterality is assumed to play an important role in stress responses in humans and non-human mammals, with much evidence pointing to right hemispheric involvement [47]. Although stress is a traditional focus point in the study of farm animal welfare [209], only a few studies have yet considered the roles of the two hemispheres during stress in ungulate livestock. There are some indications of a right hemisphere dominance, since stress induced by a simulation of sea motion was accompanied by more (ipsilateral guided) startle movements of the right leg in sheep [86], while in donkeys, stress caused by space restriction increased the (contralateral guided) use of the left forelimb while standing (as reflected by the disappearance of a population right bias [93]). Additionally, in pigs, tethering led to higher receptor density in the right hippocampal lobe [170]. The left hemisphere, conversely, may be more sensitive to the negative effects of stress, since high salivary cortisol levels in pigs after tethering correlated negatively to neuron numbers and the volume of the left dentate gyrus [171]. In addition, stress induced by intense tactile stimulation of foals directly after birth increased fear responses to humans at a later age, mostly in foals that were handled from the right side [105], suggesting that the left hemisphere is less able to cope with such stressful events. As mentioned in Section 4.4, different effects of prenatal undernutrition have also been reported. Intensively housed cattle were found to be more strongly lateralized than extensively housed cattle, suggesting that stress may result in stronger laterality [78]. However, since only one farm per system was involved and no clear differences in stress were found between the two groups, these interpretations must be treated with caution. Thus, although there are some indications of associations between laterality and stress in ungulate livestock, further investigation is required.

Due to the differential role of the two hemispheres in stress responses and the associations of laterality with different health risks in ungulate livestock, it is apparent that laterality can have important implications for animal welfare. Laterality measures can be employed in welfare assessments as a non-invasive tool to contribute to a more accurate identification of animals with diseases or at risk of injury. Individual side preferences could be taken into account to reduce stress during certain farm management procedures such as milking ([81,177], but see [83]), or in the design of housing facilities [87]. Additionally, the knowledge of lateralized processing of emotions can be used to determine from which side to approach and handle the animals [68,102,105,107,140,150]. As laterality is associated with personality, the expression of laterality may be used to identify individuals who may respond more fearfully in certain situations and thereby avoid or reduce such situations for these animals [45,46]. Thus, laterality could be used in practice to improve animal welfare. However, the indirect effects of basic knowledge of laterality in ungulate livestock on animal welfare should not be ignored herein, since such knowledge may affect consumer choices. For instance, knowledge that ungulate livestock have lateralized cognitive processing, which was originally thought to be unique to humans [210], could cause consumers to reflect on the psychological attributes of these animals. Such reflections have been found to trigger aversion to eating these animals [211]. Therefore, it is important to also advance our basic knowledge of laterality in these research fields.

4.7. Production and Performance

Production and animal welfare sometimes go hand in hand, since healthy and unstressed animals usually produce better quality products [212]. However, selection for high production efficiency has often led to impaired farm animal welfare [213]. Nevertheless, it is important to consider the effect of lateralized processing on production and performance, since this is relevant for the farmer (or in the case of sport horses, the owner) and consequently also indirectly reflects again on the welfare of the animals. Several studies have reported that cows with a left bias for different motor functions, such as lying [145,146] and passing a novel human [149], produced more milk. In contrast, a right eye preference during fighting was found to be associated with high body score conditions in cows [144]. There are also signs that the side entered in the milking parlor affects milk production, with either the left [81] or the preferred side [82] resulting in more milk yield. Rhizova and Kokorina [135] found that the side from which cows saw food arriving may affect milk production (but only under good feeding conditions), since cows that saw food always come from the left for a few months per year produced more milk during this period than cows that saw food always come from the right during the same period. In the same study, reproduction was also positively affected by left side food delivery, since the same cows also had shorter mean service periods. These results suggest that chronic presentation of an emotionally relevant stimulus may influence somatic functions and consequently improve both productive and reproductive performance. Other studies also suggest that a left bias during lying may be associated with pregnancy in cows [75,77,79,132,147], which is most likely due to the position of the fetus [78]. In horses, performance in different types of tasks such as dressage and racing was found to be associated with laterality. For instance, studies have shown that horses led from the left side (the side horses are traditionally handled from [128]) had higher trotting speeds [118] and needed less pressure to be pushed into movement [113]. However, another study found opposite results, with right-sided training resulting in faster task completion [128], which they attributed to desensitization to negative reinforcement on the left due to regular training on this side. In addition, since most sports require horses to perform symmetrically [94,97,120], strongly lateralized horses were found to require a longer period of training to even out sidedness in their performance [94]. Altogether, these findings suggest that laterality is associated with production and performance and should be taken into account in farm/sport practice. To some extent, laterality is already an important aspect of horse training, with a traditional practice to handle horses mainly from the left side [128] and an aim to achieve symmetrical performance [94,97]. However, acquired knowledge on lateralized fear responses and training success in horses [68,128] would help to adapt this practice to improve training results.

5. Future Directions

This review shows that although research on laterality in ungulate livestock is a very young research field, there have already been some interesting discoveries that will help to advance the research on laterality and other research disciplines, as well as provide potentially useful applications for practice in the future. In particular, much research has already been done on motor laterality. Currently, increasingly more studies are also investigating laterality in cognitive performance and emotional processing, as well and considering its association with personality. Research on laterality in ungulate livestock therefore has the potential to be relevant for many different research fields in basic and applied animal science, as well as in husbandry practices. However, the overview provided in this review shows that many steps are still needed before this full potential in science and practice is achieved. In science, it is important that future research further integrates basic and applied scientific methods. On the one hand, basic scientific methods to study laterality are needed for a more systematic investigation of the role of the two hemispheres. At the moment, many of the reviewed studies still lack a systematic methodology for studying laterality. For instance, many of these studies have not tested for significant individual side preferences and have used various calculations to generate a continuous measure of laterality, making it difficult to interpret the results or to compare findings. Therefore, it is important that further research on lateralized behavior in ungulate livestock integrates established laterality methods, such as repeated testing to determine individual biases, symmetrical set-ups and procedures and, most importantly, the calculation and report of significant biases at the individual and/or population level whenever possible. For the latter, standard laterality calculations and statistics are preferred, such as the z-score or binomial test to test for individual and population biases and a Laterality Index ($LI = (R - L)/(R + L)$) as a continuous measure of laterality [214]. Also, many of the reviewed studies fail to consider the role of hemispheric asymmetries that underlie the observed lateralized behavior in the interpretation of the findings, which undermines the insight that could be gained from these findings. Future studies would therefore also benefit from a better reflection on this. On the other hand, laterality research in ungulate livestock would also benefit from a better integration in applied animal research. As already briefly addressed in Section 4.5, behavioral observations of some easy-to-observe lateralized functions (e.g., forelimb preferences, ear or tail posture, or eye preferences) could be integrated in studies using established behavioral tests without requiring changes in the experimental procedure. Therefore, they could be included as additional behavioral parameters in various studies on animal welfare, such as investigations of the effects of environmental enrichment, stress, diseases, health risks, immune responses, emotional processing and many others. Initially, such an integration would induce a substantial increase in knowledge regarding the role of lateralized processing in animal welfare-related issues. Later, once the interpretation of a lateralized function with regard to animal welfare is well established, this integration would also result in the addition of a non-invasive, useful tool to assess welfare in future studies. In this way, such an integration may benefit both laterality and animal welfare research. At first, the emphasis of research on laterality in ungulate livestock should focus more on understanding the expression of functional laterality in these species. Controlled experimental settings with a symmetrical setup are particularly important for accomplishing this goal. However, once this is better understood, it becomes increasingly more important to investigate the expression of laterality in farm settings and during different farm management procedures. In this way, findings from studies in more controlled settings can be validated, and the role of lateralized processing in the daily life of ungulate livestock can be better understood. Of special interest would be to test the effect of different farming regimes [78] on lateralized processing and to investigate the role of lateralized processing in human-animal interactions (e.g., [107,150]).

At present, laterality does not yet play an important role in husbandry practices, with the possible exception of horse sports, where laterality is taken into account in training and the judgement of performance (see Section 4.7). However, as outlined in Section 4.6, laterality can have important implications for the welfare of livestock. Therefore, knowledge of laterality in ungulate livestock could ultimately be applied in practice to improve animal welfare, for instance, through an improved assessment of an animal's welfare state, a reduction of stress during human-animal interactions, a better evaluation of an individual's ability to cope with certain situations and an improved design of stalls and other structural facilities. Knowledge of laterality may also potentially help to improve performance, as outlined in Section 4.7. Therefore, it may increase the benefits for the farmer/owner and thereby reduce the necessity of increasing pressure on the animals for better profit. However, any practical application would have to be based on a thorough understanding of the specific lateralized function in the species of interest, which requires first more controlled and second more on-farm experiments, as outlined above in this section. Since for most lateralized functions in most ungulate livestock species these two steps are not yet complete or even completely missing, much work still needs to be done before knowledge on laterality can be applied in practice.

6. Summary and Conclusions

The research on functional laterality in most ungulate livestock species is still in the infancy phase and therefore offers many new opportunities for science, welfare and practice. As domestic and social species, with a precocial life history, a high degree of decussating optical fibers and well-studied emotional and cognitive processing, ungulate livestock make interesting models for laterality research.

Thus far, most studies on ungulate livestock have mainly focused on motor laterality, often without reference to the underlying brain asymmetries. Nevertheless, research on motor laterality has already shed light on the possible effects of social coordination and even domestication on the manifestation of population level laterality. Research on cognitive laterality has shown that complex social cognition skills are not unique to humans and improved our understanding of the differential involvement of the two hemispheres in social recognition. As in other non-human vertebrates, the findings on emotional laterality in ungulate livestock seem to support right hemisphere dominant processing of negative emotions such as fear and left hemisphere dominant processing of positive emotions such as responses to food. However, increasing evidence now also shows right hemisphere dominance during positive social interactions, which may challenge the emotional valence hypothesis. Findings of changes in laterality throughout the lifespan, effects of prenatal undernutrition and sex differences provide important insights in the development of laterality. In contrast, the limited number of studies on associations between laterality and personality in ungulates do not provide a clear pattern yet, with some studies showing associations of personality indices with direction and other studies with the strength of laterality. Finally, findings that some health risks, immune and stress responses and productive performance are associated with laterality provide good opportunities for applications on the farm or (in the case of horses) sport practices. Laterality assessment can be used as a tool in practice to identify individuals or situations that are at greater risk of reduced welfare. However, the overview also shows that the full potential entailed by ungulate livestock for laterality research has not yet been exploited. Future research would therefore benefit from an integration of methods and analyses from basic laterality science research (e.g., repeated testing and statistical testing of individual biases) with applied animal welfare approaches (e.g., emotionality tests and disease monitoring).

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