



Vocalisations in farm animals: A step towards positive welfare assessment

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ARTICLE INFO

Keywords:

Farm animals
Emotions
Positive welfare
Vocalisations

ABSTRACT

Public concern for farm animal welfare is increasing. Animal welfare is defined as the balance of positive and negative emotions, where positive emotions are key to a good animal life. Emotion is defined as an experience that varies in valence and arousal. Many methods developed to identify positive emotions in animals involve disadvantages. For example, they require training the animals, are age specific or invasive. Vocalisations are a promising indicator of positive emotions. We aimed to review current knowledge on farm animal vocalisations putatively associated with positive emotions and discuss the potential of vocalisations as an on-farm tool to assess positive emotions in farm animals. Vocalisation types and acoustic structures that can potentially be used to identify positive emotions depend upon species. In pigs, lower frequency vocalisations are produced more in positive situations, however, within grunts, higher frequencies reflect positive situations. In horses, more snorts and shorter, lower frequency whinnies could be linked to positive situations. In cows, closed-mouth vocalisations (lower in frequency) might be more common in positive emotions. Food calls and fast clucks may be linked to positive emotions in chickens. In goats, the fundamental frequency shows less fluctuations during positive compared to negative situations. A link between vocalisations and positive emotions has not been shown yet in sheep. Overall, a combination of vocalisations and other measures of emotions could be a promising on-farm tool to monitor positive emotions.

1. Introduction

There is a trend towards increasing public concern for animal welfare (Cornish et al., 2016). This increased concern means challenges for the future, because farmers are expected to reach continuously higher animal welfare standards. Definitions of animal welfare have varied over time following peoples' values and beliefs and following changes in our scientific understanding of animals. Most of the latest definitions promote the importance of affective experiences, i.e. the emotions and moods of animals (e.g. Fraser et al., 1997; Green and Mellor, 2011; Webb et al., 2019). Emotions and moods are affective experiences that vary in valence (pleasantness/unpleasantness) and arousal (high arousal/low arousal) (Scherer, 2005; Fraser, 2008). They can hence be conceptualised in a 2-dimensional space along the axes of valence and arousal (Russell, 1980). Emotions are considered to be relatively short-lived, intense experiences that are elicited by a specific object or event (Paul and Mendl, 2018). They are perceived as functional adaptations linked to behavioural decisions that facilitate survival and

reproduction by promoting approach towards reward and avoidance of punishment (reviewed in Kremer et al., 2020). Moods, by contrast, are considered to last longer than emotions and not be triggered by specific objects or events - moods are often referred to as free-floating - and rather constitute a running mean of emotions (Mendl et al., 2010). This review focuses on acute emotions as it is unknown whether moods can be expressed via acute vocalisations.

In the past, concern for farm animal welfare has focussed mainly on the minimisation of negative experiences (Yeates and Main, 2008). However, nowadays, there is an increased awareness amongst scientists that this approach is incomplete, does not reflect the concerns of citizens (Vigors, 2019), and that positive experiences is an important part of animal welfare as well (Yeates and Main, 2008). It has been proposed that, in order for animals to have a good or happy life, or a good quality of life, the frequency of pleasant experiences should outweigh the frequency of unpleasant experiences throughout an animal's life (FAWC, 2009; Green and Mellor, 2011; Webb et al., 2019). However, although it is developing rapidly, the research into positive aspects of welfare is far

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<https://doi.org/10.1016/j.applanim.2021.105264>

Received 17 September 2020; Received in revised form 20 January 2021; Accepted 9 February 2021

Available online 13 February 2021

0168-1591/© 2021 The Author(s).

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from being as well developed as the research into negative welfare (Boissy et al., 2007; Lawrence et al., 2019; Webb et al., 2019), and good indicators of positive emotions (i.e. reliable, fast and non-invasive) are still lacking. There is hence a need to develop valid indicators of positive emotions in farm animals and to integrate these into on-farm assessment protocols (potentially via the use of sensors). One particularly promising indicator of positive emotions is vocalisations (Manteuffel et al., 2004).

There is now substantial evidence that the production of vocalisations is affected by the emotional state of the producer. In particular, the rate of production and acoustic structure (frequencies, amplitude and duration) of vocalisations change with emotional arousal in a relatively predictive way across species; sounds are produced at faster rates, at a higher amplitude and become higher in frequency as arousal increases (Briefer, 2012, 2020). Changes occurring with emotional valence are less consistent across species, but current evidence shows that often, different types of sounds are produced in situations of opposite valence (e.g. pig grunt versus squeal; Tallet et al., 2013), and sounds that are produced in both positive and negative situations tend to be shorter and lower in frequency when the producer experiences a positive situation (e.g. affiliative interaction) compared with a negative one (e.g. negative interaction) (Briefer, 2012, 2020). Furthermore, the evidence that vocalisations are involved in emotion expression is supported by the role of the amygdala in animal vocal production (Jürgens, 1982). The amygdala is a part of the brain that is involved in both positive and negative emotions in amniote vertebrates (at least) (Martínez-García et al., 2008), including hence birds and mammals, the two groups of animals used as livestock. In addition, it has been found that vocalisation types composing the vocal repertoire of a species are produced through specific pathways originating in the amygdala (Jürgens, 1982; Hamann and Mao, 2002).

Vocalisations are well suited for the expression and communication of emotions (Manteuffel et al., 2004; Briefer, 2012, 2018). Firstly, sound can travel relatively well across obstacles, depending on its frequencies, which is for example not the case with visual expression of emotions (e.g. facial expression) (Nordell and Valone, 2017). Secondly, acoustic signals can carry over relatively long distances, meaning that conspecifics do not necessarily have to be close to perceive the information encoded in each other's vocalisations (Manteuffel et al., 2004). Finally, the acoustic structure of vocalisations can vary relatively quickly when a situation changes, which is not possible with, for example, chemical signals (Nordell and Valone, 2017). An advantage of vocalisations as indicators of farm animal welfare is that most mammals have relatively less control over their vocalisations compared to humans (Jürgens, 2009), thus the link between emotion expression and vocalisations is predicted to be even stronger than in humans (Briefer, 2012). Moreover, with the current potential for developing automated vocalisation detection systems, on-farm techniques can be developed to assess vocalisations rapidly and over long periods of time (McCloughlin et al., 2019; Herborn et al., 2020).

Animals can produce various kinds of vocalisations to express emotions. For instance, the chatter vocalisations in California ground squirrels announces the presence of a predator (Owings and Leger, 1980), while the 50-kHz ultrasonic vocalisations in rats are associated with pleasure (Rygula et al., 2012). Depending on the context, some vocalisations can thus be associated with negative emotions (e.g. in the presence of predators, during social isolation or during agonistic interactions), and others with positive emotions (e.g. in the presence of food, during social reunion or during affiliative interactions) (Brudzynski, 2013). Positive vocalisations, i.e. vocalisations produced in positively valenced situations, have an important communication function in the wild and likely also in domestic or captive settings. They may facilitate group living in social species by promoting communication, cooperation, and bond formation between individuals (Sporer and Kelly, 2004; De Waal, 2008; Špinková, 2012). It was furthermore shown in rats that vocalisations linked to positive emotions are initiated via another pathway in the brain compared to vocalisations linked to

negative emotions (Brudzynski, 2015), emphasising the existence of a distinction between the expression of positive and negative emotions in vocal expression.

Vocalisations have been studied in farm animals to some extent, yet a good overview of the various types and their function, especially in relation to positive emotions, is missing. Therefore, the aim of this systematic review was to summarize the current evidence suggesting that vocalisations could be used to identify positive emotions in farm animal species. The aim was divided into two sub-questions: 1. What aspects of animal vocalisations can be measured? and 2. Which types of vocalisations may be linked to positive emotions, within and across farm animal species? We end the review with a discussion on the amount and quality of research focussing on the link between vocalisations and positive emotions in farm animals and on the practical implementation of vocalisations as an on-farm positive emotion assessment method.

2. Methods for systematic literature review

To retrieve the articles for this review, the database Web of Science was used. The retrieved articles were selected based on relevance and categorised per sub-question. The abstracts of the articles were used to determine the relevance. Only articles in English published between 1945 and October 2019 were used.

For both sub-questions, the following search strategy was used:

	welfare OR well-being OR emotion* OR "affective state?" OR "quality of life" OR "wellbeing"
	"farm animal?" OR "barnyard animal?" OR livestock OR horse? OR mare? OR stallion? OR foal? OR cow? OR bull? OR calf OR calves OR heifer? OR cattle OR poultry OR chicken? OR turkey? OR duck? OR hen? OR rooster? OR
AND	broiler OR pig? OR swine OR boar? OR sow? OR goat? OR buck? OR doe? OR sheep OR ewe? OR ram? OR lamb? OR rabbit? OR bunny OR alpaca? OR bison? OR camel? OR donkey? OR llama? OR buffalo? OR yak? OR zebu? OR deer
AND	positive OR happy OR pleasant OR affiliat* OR "playing behavior*" OR joy OR "approach behavior"
AND	vocali?ation? OR sound OR playback OR acoustic* OR "vocal expression"

The word "kid" (baby goat) was excluded, because too many articles in this search were about human children. "?" and "*" were used to include both American and British English spelling, and singular and plural words. Some articles that turned out not to be relevant, based on reading the entire article, were excluded. This led to a total of 23 articles. Based on these selected articles, we decided to limit our review to the species pigs, horses, cows, goats, sheep and chickens, because articles on other farm animal species were absent. Additional articles were obtained both via the snowballing method and the citation method. Next to this, we conducted non-systemic searches for articles focussing on sound waves, on the physiology of the vocal tract in mammals and in birds and on applications of vocalisation measurements outside farm contexts, for more in depth information about these specific topics. This led to a total number of 79 articles (Fig. 1).

3. What aspects of animal vocalisations can be measured?

Four systems play a role in the production of a vocalisation; respiration, phonation, resonance and articulation (Titze, 1994). An emotion can affect each of these four systems (Briefer, 2012). Emotions can directly influence respiration and muscle tension and thereby affect phonation, resonance and articulation (Briefer, 2020).

According to the source-filter theory, a vocalisation is generated at a source, the vocal folds, and is then filtered by the vocal tract (Titze, 1994; Taylor and Reby, 2010). This source determines the fundamental frequency and is influenced by respiration and phonation, and thus the lungs, trachea and the larynx of an animal (Fant, 1970). In mammals, the larynx transforms airflow into sound waves. These sound waves are then filtered by the supralaryngeal vocal tract, namely the pharynx, the vocal, oral and nasal cavities, the nostrils, the lips, the tongue, the teeth

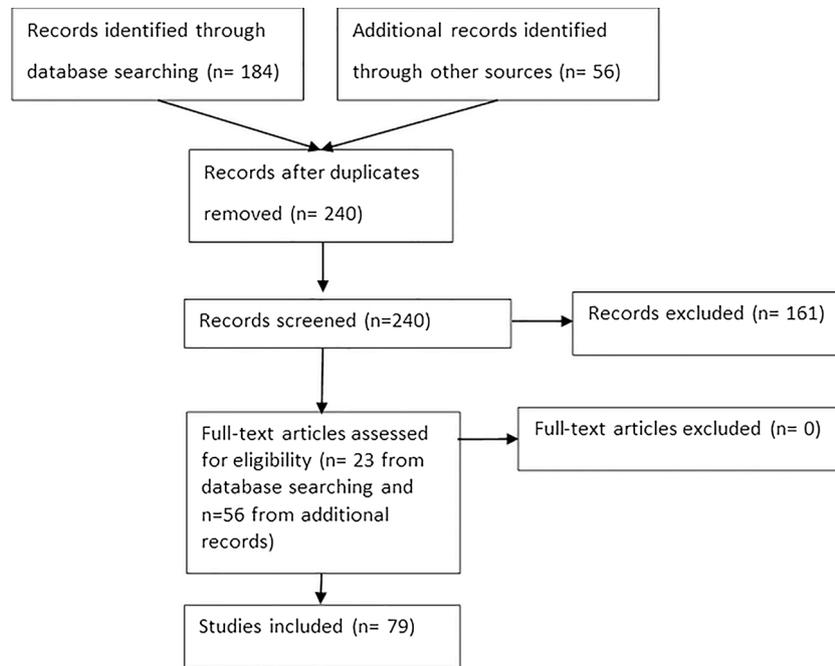


Fig. 1. Flow diagram of the selection process of the articles used for this review. Adapted from: (Moher et al., 2009).

and the jaw of the animal. During this filtering, which depends on the resonance and articulation systems, the energy distribution of a vocalisation is shaped and so-called formants are formed, i.e., some frequencies are amplified while others are dampened out (Fant, 1970; Taylor et al., 2016). The mechanism of sound generation in birds (specifically chickens) varies from mammals. Chickens use their syrinx (tracheobronchial type), which is located at the bifurcation of the trachea into the primary bronchi, to create a sound (Yildiz et al., 2003; Casteleyn et al., 2018). The lateral tympaniform membranes stretch from the tympanum (cranial part of the syrinx) to the cartilagineous bronchosyringeales (caudal part of the syrinx) (Casteleyn et al., 2018). Upon vibration of these lateral tympaniform membranes, caused by air flow, a sound is generated (Casteleyn et al., 2018). This sound is, similarly to mammals, subsequently filtered in the suprasyringeal structures (the trachea, the oropharyngeal-oesophageal cavity, the tongue and the beak) (Beckers et al., 2004; Casteleyn et al., 2018).

In each species, many different types of vocalisations can be produced, but most can be measured using a number of common parameters. Table 1 gives an overview of the parameters used in the studies included in this review, with their corresponding definition and references (for a complete overview of parameters that can be measured see Briefer, 2012). Fig. 2 displays some of these parameters for sheep bleats.

4. Which types of vocalisations reflect positive emotions, within and across farm animal species?

In this section, we describe the different vocalisation types produced specifically in putative positive contexts and thereby linked to positive emotions (hereafter called ‘positive vocalisations’), as well as the valence-related changes to the acoustic structure of vocalisations that can occur in both positive and negative emotions, along with a discussion of the interspecies differences and similarities. Whenever possible, emotional situations that differ in valence but trigger a similar level of arousal, as far as can be deduced from the recorded description, are compared to each other, in order to ensure that changes to vocalisations are not in fact due to changes in arousal instead of valence. Each farm animal species for which positive vocalisations were studied (i.e. pigs, horses, cows, goats, sheep and chickens) is first discussed separately. Thereafter, comparisons between species are made. In Fig. 3, we provide

an example of a positive vocalisation for each species considered (oscillogram and spectrogram).

4.1. Pigs

Tallet et al. (2013) proposed a five category system for the division of the different pig vocalisations: LFm, LFs, LfT, HFm and HFf vocalisations, where LF stands for low frequency, HF for high frequency, m for modulated, s for stable and t for tonal (Table 2). Differences in frequency can also be found within the LF and HF groups. For example, low grunts are LFs vocalisations (stable vocalisations with a very low frequency) and high grunts are LFm vocalisations (modulated vocalisations with a low frequency). Grunts are sometimes also divided into short and long grunts (shorter than 0.4 s or longer than 0.4 s), however it is suggested that most low grunts are long grunts and most high grunts are short grunts (Kiley, 1972; Leliveld et al., 2017). Barks can be identified as LFm or LfT vocalisations. Squeals can be both HFm and HFf vocalisations, while screams can only be categorised as HFm vocalisations (Tallet et al., 2013). Grunts (Fig. 3a) are usually expressed when a pig is eating or wandering around or by sows to indicate that piglets can suckle (Algers and Jensen, 1985). Grunts can, however, also be produced during negative situations with a similar arousal level as the positive situations, e.g. both in the negative/punished trials in a cognitive bias test and the positive/rewarded trials (Kiley, 1972; Briefer et al., 2019; Friel et al., 2019). Thus, it can be said that grunts are produced in various negative and positive situations. Barks appear to play a role both as an alarm call and during play behaviour; they are thus produced both in negative and in positive situations as well, which are likely higher in arousal compared to situations triggering grunts (Kiley, 1972; Chan et al., 2011; Reimert et al., 2013). Squeals and screams are higher in pitch and amplitude than grunts (Kiley, 1972). The difference between a squeal and a scream is the continuity of the fundamental frequency (‘F0’) (Kiley, 1972). In screams, the F0 is constantly changing, while it is more stable in squeals (Kiley, 1972). Screams are very loud and occur when a pig is experiencing a negative emotion (Kiley, 1972). Squeals are expressed by sub-adult pigs, mainly in negatively valenced situations of high arousal (Kiley, 1972). Situations in which squeals and screams are expressed are sometimes similar, for example when a pig is experiencing pain or social isolation (Kiley, 1972). However, squeals are also

Table 1

Parameters of vocalisations described in the studies used in this review, with their definitions and corresponding references.

Parameter	Definition	References to studies described in this review
Duration	The duration of a vocalisation.	(Briefer et al., 2015a; Maigrot et al., 2018; Briefer et al., 2019; Friel et al., 2019)
Vocalisation rate	The number of vocalisations in a certain time frame.	(Stěhulová et al., 2008; Imfeld-Mueller et al., 2011; Briefer et al., 2019)
F0	The fundamental frequency and its contour (e.g. min, mean, max and range).	(Briefer et al., 2015a, b; Leliveld et al., 2016; Riley et al., 2016)
FMextent	The variation between two peaks of each F0 modulation in Hz.	(Briefer et al., 2015b)
Bandwidth	The difference between the highest and lowest observed frequency (Hz).	(Leliveld et al., 2016)
Amplitude	Level of energy in the vocalisation, the intensity of a vocalisation (decibel).	
AMextent	The mean-to-mean peak variation of each amplitude modulation (decibel).	(Briefer et al., 2015a; Maigrot et al., 2017)
AMrate	The number of amplitude modulations in a certain time frame.	(Maigrot et al., 2018)
AMVar	The cumulative variation in amplitude divided by the duration of a vocalisation (dB/s).	(Briefer et al., 2015a)
Q25 %	The frequency below which 25 percent of the energy is contained (Hz).	(Briefer et al., 2015a; Leliveld et al., 2016; Maigrot et al., 2017, 2018)
Q50 %	The frequency below which 50 percent of the energy is contained (Hz).	(Briefer et al., 2015a; Leliveld et al., 2016; Maigrot et al., 2018)
Q75 %	The frequency below which 75 percent of the energy is contained (Hz).	(Briefer et al., 2015a; Maigrot et al., 2017, 2018)
Formants	Frequencies that correspond to the resonances of the vocal tract.	
F1mean, F2mean, F3mean, F4mean	The mean frequency of each formant (Hz).	(Maigrot et al., 2018)
F1, F2, F3 and F4 range	The frequency range of each formant, thus the difference between the maximum and minimum frequency of that formant (Hz).	(Maigrot et al., 2018)
Fpeak	The frequency of peak amplitude.	Fig. 2

expressed during startling stimuli and anticipation of a positively or negatively valenced stimulus, where screams are not expressed (Kiley, 1972). Furthermore, boars express ‘courting songs’ around mating, which, among others, aim at eliciting a standing reflex in sows (Hughes et al., 1985).

Across studies, the overall expression of vocalisations (low and/or high frequency vocalisations) seems to be higher in negative compared to positive situations. Imfeld-Mueller et al. (2011) found that the total number of high frequency vocalisations was higher when anticipating a negative event (crossing a ramp) compared to a positive event (food-reward), although this was not the case for low frequency vocalisations. By contrast, Briefer et al. (2019) found that the number of low frequency vocalisations was higher in a negatively valenced situation (social isolation) compared to a positively valenced one (being in a test arena with a conspecific, food and toys). The F0 of vocalisations increases in piglets in a stressful situation, e.g. being captured, compared to a situation in which the caretaker greets the piglets (assumed to be a positively valenced situation) (Riley et al., 2016). The F0 decreases when the piglets anticipate that this stressful situation will come to an end (when lowering the piglets to put them back into the pen). It should be noted however that this is not necessarily a positively valenced situation but rather a less negatively valenced one (Riley et al., 2016). In adult pigs, grunts are produced in both positively and negatively valenced situations, and the valence affects their acoustic structure. In positively valenced situations, grunts are characterised by shorter durations compared to negative situations of similar arousal (e.g., short social isolation, or receiving no reward during the negative trial of a cognitive bias test) (Briefer et al., 2019; Friel et al., 2019). In addition to that, when young pigs (4–7 weeks old) produce grunts while experiencing positive emotions (i.e., receiving a reward), the bandwidth, maximum frequency, Q25 % and Q50 % are higher compared to when they are experiencing negative emotions (i.e., getting startled) (Leliveld et al., 2016). This means that the grunts in positive situations are characterised, in general, by higher frequencies (Leliveld et al., 2016).

In addition to this, some research has been carried out in adult wild boars (Maigrot et al., 2018). It is not known if these results can be generalised to the adult domesticated pig, because changes in vocalisation could have occurred during domestication (Maigrot et al., 2018). Nevertheless, the domesticated pig is closely related to the wild boar (Larson et al., 2005), and that is why these wild boar findings are

presented here. In wild boars, Q25 %, Q50 %, Q75 %, duration, F2mean, F2range, F3mean and F3range increase from putatively positively valenced situations (food reward and affiliative behaviour) to negatively valenced situations (agonistic interactions) (Maigrot et al., 2018). These parameters reflect the frequency and duration of a vocalisation, thus it can be said that wild boars produce lower frequency vocalisations that are shorter in duration when experiencing positive emotions (Maigrot et al., 2018). In addition, AMrate was found to be lower in the positively valenced compared to negatively valenced situations (Maigrot et al., 2018). In other words, modulations in amplitude during one vocalisation are slower in positive situations than in negative ones (Maigrot et al., 2018).

To summarise, in pigs it seems that during various positively valenced situations more low frequency vocalisations with a shorter duration are produced (Imfeld-Mueller et al., 2011; Friel et al., 2019). However within grunts, positive situations are related to higher frequencies, suggesting that valence-related changes to the structure of vocalisations might vary between call types (Leliveld et al., 2016).

4.2. Horses

Horses produce both vocal and non-vocal sounds (Stomp et al., 2018a). The difference between these two types of sounds is that the larynx plays a role during the production of vocal sounds and not during the production of non-vocal sounds (Yeon, 2012). The main vocal sounds include squeals, nickers and whinnies (Table 3) (Yeon, 2012). A squeal is a loud, high-frequency vocalisation that contains few amplitude modulations (Maigrot et al., 2017). A nicker (Fig. 3b) is a short, pulsated and low-frequency vocalisation (Maigrot et al., 2017). Finally, a whinny starts with a squeal-like sound and ends with a nicker-like sound (Maigrot et al., 2017), so is in essence a combination of the first two vocalisation types. Whinnies have the particularity that they contain two partially independent fundamental frequencies termed ‘F0’ (lower one) and ‘G0’ (higher one), suggesting biphonation (Briefer et al., 2015a). Non-vocal sounds include snores, blows and snorts (Table 3) (Stomp et al., 2018a). The snore is produced during inhalation, while the blow and the snort are produced during exhalation through the nostrils (Stomp et al., 2018b). The difference between a blow and a snort is that a blow is non-pulsated, while some, but not all snorts are pulsated and snorts have a longer minimum duration (490–1310 ms) compared to

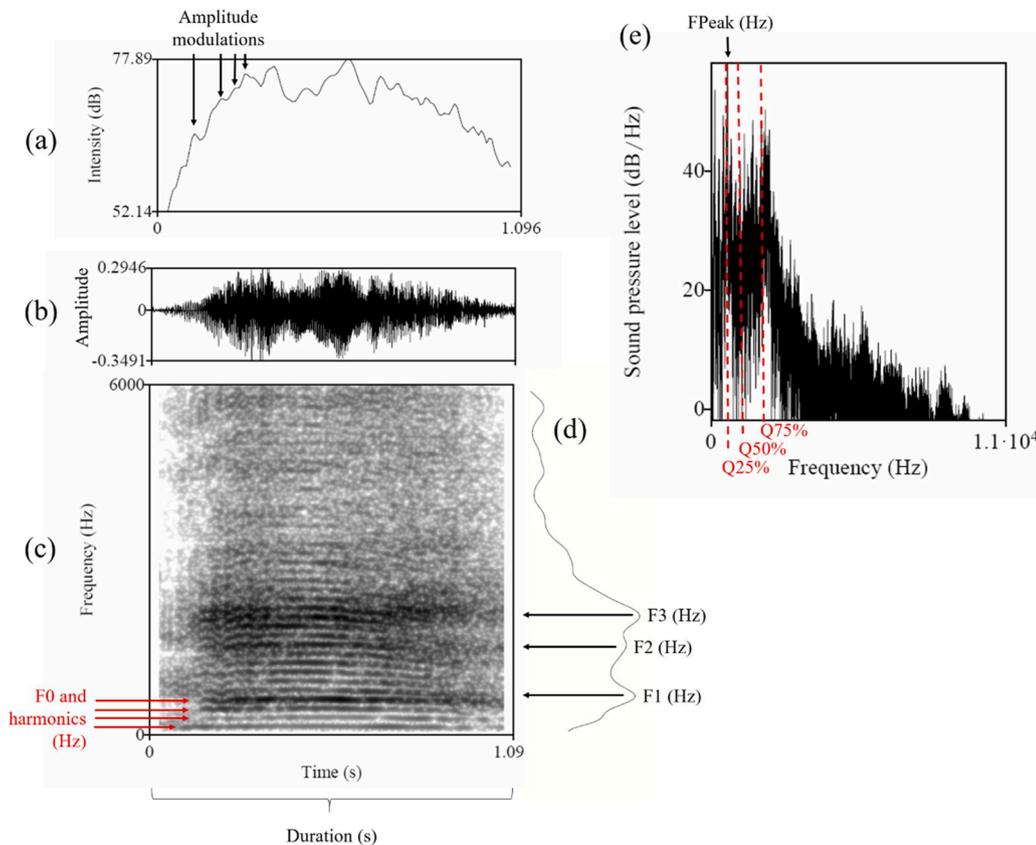


Fig. 2. Illustration of the main acoustic parameters that can be measured in farm animal vocal sounds (here a sheep bleat). (a) Intensity contour (intensity (dB) as a function of time (s)) showing the first four amplitude modulations (AM); (b) Oscillogram (relative amplitude as a function of time (s)); (c) Spectrogram (frequency (Hz) as a function of time (s)) showing the duration (below) and the fundamental frequency (F0) and its first three harmonics (in red); (d) Spectral smoothed spectrum (frequency (Hz) as a function of sound pressure level (dB/Hz)) showing the first three formants, which are also visible on the spectrogram; (e) Spectrum (sound pressure level (dB/Hz) as a function of the frequency (Hz)) showing the peak frequency (FPeak) and the energy quartiles (in red: Q25 %, Q50 % and Q75 %). See Table 1 for definitions of the parameters.

blows (340–1300 ms) (Yeon, 2012; Stomp et al., 2018b).

Squeals are almost exclusively produced in negative situations (Yeon, 2012). By contrast, nickers are produced in three main situations: when horses anticipate a positive stimulus such as reunion with a conspecific or feeding, when mares warn their foals of danger (negatively valenced) and when a stallion encounters a mare in oestrus (positively valenced) (Yeon, 2012). According to the research of Maigrot et al. (2017) on the closely related Przewalski's horses, nickers are also occasionally, although rarely, expressed during agonistic interactions and during social separation. The nickers produced in differently valenced situations can also be distinguished from each other in this species, by having a higher Q25 % and AMextent in positive situations (i. e., anticipation of a reward and affiliative interactions) compared to negative situations (i. e., social separation and agonistic interactions) (Maigrot et al., 2017). It is unknown whether these results can be generalised to all horses, because there are differences in vocalisations between Przewalski's horses and domestic horses (Maigrot et al., 2017). In Przewalski's horses, when combining all vocalisations together, Q75 % increases from positively to negatively valenced situations after controlling for variation in arousal (Maigrot et al., 2017).

Whinnies are produced in both positive and negative situations, for example during separation and reunion with conspecifics (Yeon, 2012). The whinnies produced in differently valenced situations can be distinguished (Pond et al., 2010; Briefer et al., 2015a). The duration, G0 at the start of the vocalisation, G0max, G0mean, F0max, Q25 %, Q50 % and Q75 % all decrease in positively valenced situations compared to negatively valenced ones (Briefer et al., 2015a). On the other hand, the AMextent and the AMvar are higher in positively compared to negatively valenced situations (Briefer et al., 2015a). In other words, whinnies produced in positive situations are characterised by a shorter duration, are lower in frequency, and have more and larger amplitude changes compared to negative situations (Briefer et al., 2015a).

Snores seem to be a stress-releasing behaviour (snoring might restore

heart-rate activity back to basal levels following negatively valenced situations) and blows may be linked to vigilance (e.g. blows are produced in the presence of fear-inducing objects) (Scopa et al., 2018; Stomp et al., 2018b). Snorts have been proposed as an indicator of positive emotions in horses, as they are for example produced during eating (Stomp et al., 2018b). An alternative explanation is that these sounds could function to clean the nostrils of dust during eating (Yeon, 2012). The two types of snorts, pulsated and non-pulsated, are both produced in putative positive situations, however the pulsated snorts are most prominent in highly positive situations (i.e. getting access to pasture) (Stomp et al., 2018a).

Overall, it seems that nickers (although occasionally expressed during negatively valenced situations), short whinnies and snorts may be linked to various positively valenced situations, though further research is required here to disentangle positive emotion from functional uses of sounds, such as cleaning nostrils. Some of the studies cited here are, moreover, observational and experimental work is thus warranted to confirm the link between these sounds and positive emotions in horses. Finally, the vocalisation parameters reflecting emotional valence in horses might, as suggested for pigs, differ between vocalisation types.

4.3. Cows

In cows, vocalisations were originally described as being built from four "syllables", 'm', 'en', 'en' and 'h' (Kiley, 1972). The 'm' syllable is produced with a closed mouth, while both the 'en' syllables are produced with an open mouth. The 'h' syllable can be produced both with an open or closed mouth (Kiley, 1972). The difference between the two 'en' syllables is the frequency, one syllable is twice as high as the other. Together, these syllables form the different vocalisations (Kiley, 1972). The sound 'mm' constitutes a contact vocalisation between different members of a herd, between mother and calf or during food frustration (no reward) (Kiley, 1972). 'men(h)' vocalisations are expressed in

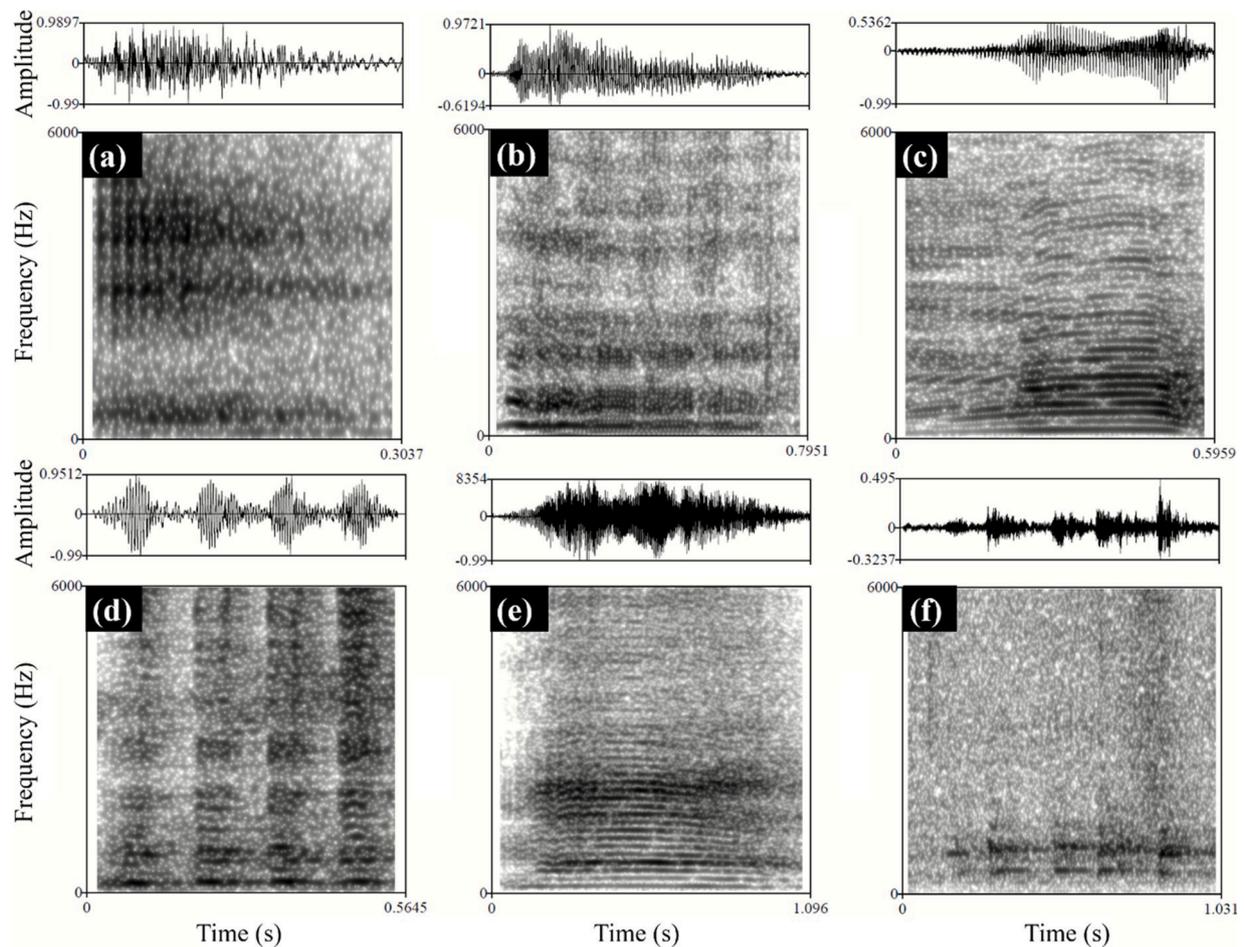


Fig. 3. Examples of positive farm animal sounds. Oscillograms (above) and spectrograms (below; window length = 0.02 s, view range = 0–6000 Hz) of (a) a pig closed-mouth grunt produced while exposed in pairs to a familiar environment with toys, food and water (Briefer et al., 2019); (b) a horse nicker produced during social reunion with pen mates (Briefer et al., 2015a); (c) a cow open-mouth call produced upon reunion with her calf (Padilla de la Torre et al., 2015b); (d) a closed-mouth goat bleat produced during food anticipation (Briefer et al., 2015b); (e) a sheep open-mouth bleat produced during social reunion with a pen mate (Lefevre et al., In preparation); (f) a chicken fast cluck from a hen produced during reward anticipation (McGrath et al., 2017). Note that the y-axis of spectrograms is the same across sounds (range = 0–6000 Hz), while the x-axis (time) varies.

Table 2

Pig vocalisations and the corresponding vocalisation characteristics according to the five category system of Tallet et al. (2013).

Pig vocalisation	Vocalisation characteristics
Low grunts (closed mouth)	Low frequency, stable (LFs)
High grunts (open mouth)	Low frequency, modulated (LFm)
Barks	Low frequency, modulated or tonal (LFm or LFt)
Squeals	High frequency, modulated or stable (HFm or HFt)
Screams	High frequency, modulated (HFm)

similar situations as ‘mm’ vocalisations, however the arousal of the stimulus is often higher (see Fig. 3c for an open-mouth men(h) sound following reunion with the calf). For example, ‘men(h)’ vocalisations are expressed when a cow is reunited with the herd after social isolation, while an ‘mm’ vocalisation is produced to remain in contact while present in the herd (Kiley, 1972). ‘(m)enh’ vocalisations are also expressed in similar situations, but which persist over a longer duration compared to situations where ‘mm’ and ‘men(h)’ vocalisations are produced. An example of such a situation is calling of the mother after separation from the calf, while she can hear the calf calling back (Kiley, 1972). The ‘menenh’ vocalisation is again expressed in a similar situation, but with an even higher intensity, such as social isolation. In addition to these vocalisations, the ‘see-saw’ vocalisation is solely produced by bulls, for example when they see two other animals fight

Table 3

The different types of horse vocalisations and the corresponding vocalisation characteristics (Yeon, 2012; Briefer et al., 2015a; Maigrot et al., 2017; Stomp et al., 2018a, b).

Horse vocalisation	Vocalisation characteristics
Squeals	Loud, high frequency, few amplitude modulations
Nickers	Short, pulsated, low frequency
Whinnies	Start with a squeal-like sound and end with a nicker-like sound, biphonation
Snores	Non-vocal, during inhalation
Blows	Non-vocal, during exhalation, non-pulsated, shorter minimum duration compared to snorts
Snorts	Non-vocal, during exhalation, sometimes pulsated, longer minimum duration compared to blows

(Kiley, 1972). These vocalisations consist of repeated ‘menenh’ vocalisations with short intervals between the vocalisations (Kiley, 1972).

Nowadays, cow vocalisations are more often divided into low frequency and high frequency vocalisations (Padilla de la Torre et al., 2015a). The low frequency vocalisations (consistent with the ‘mm’ vocalisations described by Kiley) are produced with a closed or partially opened mouth and are, for example, expressed by the mother when her calf is in close proximity (Padilla de la Torre et al., 2015a). On the other hand, high frequency vocalisations are produced with an opened mouth

and are, for example, expressed when the mother is separated from her calf (Padilla de la Torre et al., 2015a).

Little research has been carried out on the effect of emotional valence on cow vocalisations. This might be because the occurrence of vocalisations is often low in positively valenced situations in this species (Santos et al., 2019). It seems that vocalisations do occur more often when a cow experiences an aversive event compared to less aversive ones (Grandin, 1998). Research that was conducted in a slaughter-house showed a high vocalisation rate when an electric prod was used excessively to make the cows move (Grandin, 1998). The use of an electric prod is a highly arousing event, which activates notably the HPA-axis (hypothalamic-pituitary-adrenal axis) (Benjamin, 2005). This suggests that the results of Grandin (Grandin, 1998) could be more linked to emotional arousal than to valence. In addition, directly after separation of calf and mother (a stressful event), the vocalisation rate of the mother increases (Stěhulová et al., 2008). This increased vocalisation rate can persist for several hours after separation. When the cows are able to see their calves after separation, the vocalisation rate is higher compared to when they are not able to see their calves (Stěhulová et al., 2008). However, this increase in vocalisation rate cannot be linked to valence solely, because the separation of calf and mother also results in changes in arousal level (e.g. increased heart rate levels) (Stěhulová et al., 2008; Lv et al., 2018). Furthermore, during lying and rumination, cows make vocalisations that are lower in frequency compared to other situations, such as when a cow is feeding, stressed or expressing sexual behaviour (Meen et al., 2015). This production of low frequency sounds, also called ‘murmuring’, might be an indicator of positive, low arousal emotions in cows, although more studies should be conducted to validate these findings (Meen et al., 2015). Finally, Green et al. showed that high frequency vocalisations can be produced both during negative situations (denied feed access and physical and visual social isolation) and positive situations (during oestrus and anticipation of feed), and that vocal individuality in these calls pertains across valence (Green et al., 2019).

In calves, some evidence was found that vocalisations reflect emotions as well; during negative situations (e.g. when calves are hit or shouted at during weighing), calves vocalise more often than in less negative situations (e.g. when the handler moves slowly and does not hit and shout at the calves during weighing), suggesting that such vocalisations indicate distress (Destrez et al., 2018). We personally noticed that calves sometimes produce short vocalisations during playing, but no research on this specific vocalisation has yet been carried out to our knowledge.

To summarise, cows produce vocalisations more often during negatively valenced compared to positively valenced situations, nonetheless ‘murmuring’ calls during lying and rumination might be an indicator of positive, low arousal emotions in cows.

4.4. Goats

Goats produce two main types of bleats, open-mouth bleats and closed-mouth bleats (Lenhardt, 1977). In Fig. 3d, an open-mouth bleat produced during food anticipation is shown. Goats also produce gobbles (during sexual behaviour) and alarm snorts, but these occur much less frequently (Shank, 1972; Lenhardt, 1977). The amount of research done on the relation between valence and vocalisations in goats is limited. Open-mouth bleats can be expressed when a goat is in pain or in other negative situations, as well as in positive situations such as during food anticipation (Fig. 3d) (Lenhardt, 1977). More generally, bleats are used to keep in contact with other goats (Lenhardt, 1977). Furthermore, it has been found that FMextent and F0range of both closed- and open-mouth bleats are lower when a goat experiences positive emotions (i.e., during anticipation of a food reward) compared to when a goat experiences negative emotions (i.e., food related frustration or isolation from conspecifics) (Briefer et al., 2015b). In other words, the fluctuations in fundamental frequency seem less pronounced during positive emotions related to food reward in goats (Briefer et al., 2015b).

4.5. Sheep

Sheep produce both high frequency (open mouth; Fig. 3e) and low frequency (closed mouth) vocalisations (Dwyer et al., 1998). These low frequency vocalisations, also called ‘rumbles’, are mainly expressed by the ewe in the presence of her lamb (Dwyer et al., 1998). These vocalisations act as contact and recognition signal, but may also play a role in strengthening the bond between ewe and lamb (Dwyer et al., 1998). High frequency vocalisations are expressed in high arousal, negatively valenced situations, i.e. when in social isolation or when the ewe is separated from her lamb (Kiley, 1972; Romeyer and Bouissou, 1992; Dwyer et al., 1998). High frequency bleats can also occur in positive high arousal situations (e.g. social reunion following separation; Filippi et al., 2021; Fig. 3e). Due to a lack of research, it is not known if sheep vocalisations also change with emotional valence. Since vocalisations occur more often in negative situations compared to positive ones, it has been suggested that the vocalisation rate can be used to identify negative emotions in sheep (Greiveldinger et al., 2007; Tamioso et al., 2017). However, a change in vocalisation rate could also be linked to changes in arousal instead of valence. Thus, there is still a gap of knowledge on whether vocalisation parameters other than vocalisation rate could indicate positive emotions in sheep (Tamioso et al., 2017).

4.6. Chickens

Chickens produce many different vocalisation types, including various types of alarm vocalisations, but also vocalisations related to food (Jones, 1986; McGrath et al., 2017). Roosters produce food calls upon discovering food, and express more food calls and at faster rates when the food is highly appreciated compared to less appreciated (Marler et al., 1986). When a food reward is of lower quality, it takes longer before a rooster vocalises and it also vocalises less often (Marler et al., 1986). Such vocalisations related to food quality have not been described in other farm animal species (Marler et al., 1986). Hens also produce similar food calls, however these calls could act more as social calls, because they express them more in social situations, whether food is present or not (Evans and Marler, 1994; McGrath et al., 2017). The food call is one of the eight main vocalisations that chickens produce. The others are single clucks, double clucks, fast clucks (Fig. 3f), whines, gakel calls, singing and mixed vocalisations (Table 4) (McGrath et al., 2017). As the name suggests, single and double clucks are short vocalisations that consist of respectively one or two syllables (McGrath et al., 2017). Food calls can be described as several short clucks produced one after the other, with a low F0 and a fast rhythm (McGrath et al., 2017). Fast clucks are similar to food calls, but with a less stable F0 and rhythm (McGrath et al., 2017). Whines are longer compared to gakel calls (longer than 2.5 s) and they have a high F0 and a large frequency range (McGrath et al., 2017). Gakel calls also have a large frequency range and

Table 4

The different types of chicken vocalisations and the corresponding vocalisation characteristics (Collias, 1987; Zimmerman et al., 2000; McGrath et al., 2017).

Chicken vocalisation	Vocalisation characteristics
Food calls	Short clucks produced one after the other, low F0, fast rhythm
Single clucks	Duration of one syllable
Double clucks	Duration of two syllables
Fast clucks	Short clucks produced one after the other, less stable F0 and rhythm compared to food calls
Whines	High F0, large frequency range, longer in duration than gakel calls
Gakel calls	Large frequency range, noisy and harsh tone, first an elongated syllable followed by multiple syllables of shorter duration
Singing	Syllables with a long duration that are produced rapidly one after the other
Mixed vocalisations	High structural variability

additionally a harsh, noisy tone (McGrath et al., 2017). During a gakel call, an elongated syllable is produced first, followed by a few short syllables (Zimmerman et al., 2000). Singing consists of syllables with longer durations compared to syllables of food calls (Collias, 1987). During singing, the syllables are rapidly produced one after the other (Collias, 1987). Finally, mixed vocalisations have a high structural variability and cannot be categorised into one of the previously mentioned vocalisation types (McGrath et al., 2017).

Information about the link between valence and the different vocalisations is only present for gakel calls, fast clucks and food calls. Gakel calls are typically produced when a chicken experiences frustration (e.g., food frustration) (Zimmerman et al., 2000). In addition to that, gakel calls are produced less often in anticipation of a food reward (positively valenced) compared to a neutrally valenced situation (Zimmerman et al., 2011). Fast clucks and food calls are produced during the anticipation of a reward, which suggests that these two vocalisations might be an indicator of positive emotions (McGrath et al., 2017). In other words, chicken vocalisations related to positive emotions in reward situations seem to be rhythmic, short vocalisations, which can have variable F0 and rhythms. However, more research on how the different vocalisation parameters are influenced by valence is needed.

4.7. Interspecies similarities and differences

The existence of similarities between species in emotion expression was suggested by Darwin as early as 1872 (Darwin, 1872). Since then, interspecies similarities in vocal expression of motivational states have been observed in numerous species of mammals and birds (Collias, 1960; Morton, 1977; August and Anderson, 1987). Morton's motivational-structural rules theory suggests that the motivation of the animal influences the vocalisations it produces (Morton, 1977); in more hostile situations, the vocalisations are predicted to have a low frequency and a large bandwidth (large frequency range), while during more friendly (i.e. affiliative) or more fearful or appeasing situations, vocalisations are expected to be more pure-tone and higher in frequency (Morton, 1977). In addition to that, vocalisations that reflect friendliness (e.g. produced during affiliative interactions such as grooming) or fear (i.e. negative emotional reaction to the perception of danger, Boissy, 1998) are more likely to increase in frequency during the vocalisation, while hostile vocalisations (i.e. produced during aggressive encounters) decrease in frequency during the course of the vocalisation (Morton, 1977). Fear and hostility are both high arousal and negatively valenced, while friendliness occurs during positive social interaction and may thus be linked to a high or low arousal, positively valenced emotion (Mendl et al., 2010).

However, these motivational-structural rules can only be applied when animals are close to each other (Morton, 1977). If animals are further apart, they will adapt their vocalisations to make them travel over longer distances (Morton, 1977). A disadvantage is that this theory

cannot make a distinction between friendly and fearful situations. To allow this distinction, August and Anderson (August and Anderson, 1987) later proposed that friendly contexts are associated with more soft, low frequency sounds, such as the "purr" of Carnivora (Peters, 1984).

In contrast to Morton's motivational-structural rules theory, but in accordance with the suggestion of August and Anderson, whinnies produced by horses have a lower frequency in positive situations compared to negative ones (Briefer et al., 2015a). In line with this, pigs and cows also produce lower frequency vocalisations while experiencing positive emotions (Table 5) (Meen et al., 2015; McGrath et al., 2017).

The existence of similarities between species in how emotional valence and arousal are expressed in vocalisations has also been suggested by Briefer (2012). Overall, the evidence seems to suggest that positive vocalisations are usually shorter, with a lower and less variable F0 across species (Briefer, 2020). Accordingly, pigs, horses and chickens produce vocalisations with shorter durations during positive situations (Table 5) (Briefer et al., 2015a; McGrath et al., 2017; Friel et al., 2019).

Current knowledge suggests that expression of emotional valence is rather species specific, unlike expression of emotional arousal that has been largely conserved throughout evolution (Briefer, 2020). Indeed, vocal expression of emotional arousal mainly depends on the effect of physiological arousal on the vocal production mechanisms, which can be expected to be similar across species due to well-conserved stress pathways (Filippi et al., 2017). By contrast, expression of emotional valence might be more strongly affected by species-specific communication codes (Briefer, 2012). As a result, differences between species also exist. For example, some species are more vocal during positively valenced situations than other species. Compared to pigs and horses, sheep and cows do not produce many vocalisations when in positive situations (Tamioso et al., 2017; Santos et al., 2019), despite all species being social and hence supposedly benefitting from communication of positive emotions. In these species, a reduction from vocalisations, more than specific vocalisations types, might indicate the presence of positive emotions.

Overall, it can be said that there are interspecies similarities, but also differences. By understanding these similarities and differences, statements can be made about the generalisability of the use of specific vocal parameters as indicators of positively valenced emotions between species. However, currently that is not yet possible as gaps in knowledge are still present in all farm animals.

5. General discussion

The present review aimed to answer the following two questions: 1. What aspects of animal vocalisations can be measured? and 2. Which types of vocalisations reflect positive emotions, within and across farm animal species?

The acoustic structure of vocalisations could potentially be used to

Table 5

Acoustic characteristics of vocalisations, and vocalisation types associated with positive emotions for each farm animal discussed in this review and the generalisability of the use of these vocalisations for each species, expressed as the amount of situations used to measure the positive vocalisations.

Animal	Acoustic characteristics of vocalisations associated with positive emotions	Vocalisations types mostly associated with positive emotions	Putatively positively valenced situations used to measure (the characteristics of) the positive vocalisations
Pigs	Shorter, lower frequency (except for grunts in which the frequency is higher in positive than negative situations)	–	Food reward, toy provision, straw provision and affiliative behaviours
Horses	Shorter, lower frequency, higher AMextent and AMvar	Nickers, possibly snorts	Food reward, affiliative behaviours, social reunion and access to pasture
Cows	Lower frequency	Possibly 'murmuring' calls	Lying & ruminating
Goats	Less variable F0	–	Food reward
Sheep	?	–	–
Chickens	Shorter, more rhythmic	Food calls and fast clucks	Food and non-food reward

identify positive emotions, and might hence constitute a promising, non-invasive indicator of positive emotions. However, research on this topic is still rather limited. Here, we conclude that measurements of vocal parameters can be useful in the assessment of positive emotions in some farm animals, namely pigs, horses and maybe in cows, goats and chickens. This finding is in line with the suggestion of Boissy et al. (Boissy et al., 2007) that vocalisations could be a useful tool for on-farm assessment of positive welfare. The next part of this discussion is divided into three sections: the amount of evidence per farm animal species, the practical use and applications of vocalisation measurement techniques, and recommendations for future research.

5.1. The amount of evidence per farm animal species

The research on positive emotions and their corresponding vocalisations is still quite limited (Table 6).

The attention that is given per farm animal is not equally distributed. So far, most research has focussed on pigs and, to a lesser extent, on horses. In both pigs and horses, all articles concluded that there is a relationship between positive emotional valence and vocalisations and that this relationship can be assessed (Table 6). The evidence for pigs is stronger compared to that of horses, because more experimental research has been carried out on pigs as opposed to observational research (Table 6). Based on these results, it can be said that there is good evidence in pigs, and some evidence in horses, that positive emotions can be assessed via vocalisation measurements.

Mixed results are found in cows, with one out of two articles indicating a relationship. At this moment, the evidence is thus still weak, however future research might show that positive emotions can be assessed via vocalisation measurements in cows as well. In chickens, two out of two articles show a measurable relationship between positive emotions and vocalisations. However, this number of studies is still very limited and more research is needed in the future to support the claim that positive emotions can be measured via vocalisation in this species. In sheep and goats, so far only one study has been conducted on each species. Thus, for these farm animals, no claims can yet be made about the relationship between positive emotions and vocalisations. In the sheep study, a relationship between positive emotions and vocalisations was even absent. Note that three studies (Table 6) did not use any further putative indicator of positive emotion to confirm that positive emotion was successfully induced and some studies only used indicators of arousal or indicators for valence that are not yet well-established in literature. The evidence that the contexts studied induced positive emotion is hence limited in these studies. Therefore, there is a clear need for further research concerning the relationship between vocalisations and positive emotions in farm animals.

5.2. The practical use and applications of vocalisation measurement techniques

As was concluded from the previous section, more research and validation across contexts is necessary before vocalisations could be used to identify positive emotions in all farm animals. However, in some farm animals, the structure of some vocalisations seems to be a promising tool for on-farm positive emotion assessment. Vocalisations can be measured in a non-invasive way, since microphones can be placed in a barn without directly affecting the animals (Manteuffel et al., 2004; Whitham and Miller, 2016). In addition to that, it is possible to measure the vocalisations in a continuous way, and therefore emotion-related changes over time could be detected (Manteuffel et al., 2004).

Nevertheless, due to large intraspecies variation, it should be taken into account that there are usually pronounced differences in acoustic parameters between individuals (Manteuffel et al., 2004; Briefer and McElligott, 2011). This does not necessarily need to be a problem when changes in vocal parameters, rather than the absolute levels of these parameters, are measured. Moreover, when animals are kept outside, or

in noisy indoor environments, it will be more challenging to perform automated analysis of vocalisations, due to the presence of background noise (Stomp et al., 2018a). This background noise can, fortunately, partially be filtered out by using, for example, a parabolic reflector (Stomp et al., 2018a). In addition to that, when a microphone is placed in a barn, only measurements of the group as a whole might be possible (Reimert et al., 2013; Herborn et al., 2020). Therefore, if the state of one animal deviates from the group, it might not be detected using vocalisations at group level. Nevertheless, the source of a vocalisation can be determined with the help of a specialised microphone or by using multiple microphones and a method of sound triangulation (Matthews et al., 2016). Alternatively, automated measurements of vocalisations collected using collar-mounted acoustic recording units could be used to allow individual assessment (O'Bryan et al., 2019). Furthermore, various machine learning techniques can be applied for, amongst others, the identification of different vocalisation types (McLoughlin et al., 2019).

Automated measurements of vocalisations to identify positive emotions in farm animals have, to our knowledge, not yet been applied on farms. However, sound measurements are already used, for example, to identify pig coughs as indicator of respiratory diseases, as well as to analyse rumination in dairy cows (Moshou et al., 2001; Schirmann et al., 2009). In addition to that, some slaughter-houses do make use of sound-based techniques that assess emotions, in order to reduce the stress levels of the animals, and therefore high arousal, negatively valenced situations (Stocchi et al., 2014; Iulietto et al., 2018). With this method, the vocalisations are measured with a so-called Noise Meter app on smartphones (Iulietto et al., 2018). The use of smartphones is promising, especially if these apps are developed further to enable the simultaneous measurement of multiple vocal parameters. Despite the fact that these techniques have not yet been applied on-farm, they are very promising, especially when applied in combination with other techniques to measure emotions. Because animals do not vocalise constantly (e.g. in low arousal states), it is important to use a combination of techniques to be able to measure the emotions of an animal in every situation (Manteuffel et al., 2004). Such techniques could also focus on changes in the rate of production of specific vocalisation types over time.

5.3. Recommendations for future research

Today, it is well accepted that the presence of positive emotions is of great importance for animal welfare (Yeates and Main, 2008). Techniques to measure animal vocalisations are also well established (e.g. Taylor and Reby, 2010). Nevertheless, for farm animals, and particularly for cows, goats and chickens, it remains unclear which vocalisation types and parameters vary with emotional valence. For other species, such as sheep, the link between vocalisations and positive emotional valence has not yet been shown. Due to the limited amount of research and the large variability within and between species, it is not yet possible to generalise results found in one farm animal species to other species (Manteuffel et al., 2004; Briefer and McElligott, 2011). Thus, the application of the results from this review are limited to the farm animal species described. Moreover, some vocalisation parameters have only been measured in specific situations (such as during the anticipation of a food reward) and to increase the generalisability of the findings, there is need for future research on how these vocalisation parameters change across different positively valenced situations. Furthermore, future research could combine naturalistic observations with experimental conditions that allow emotional valence to be manipulated while controlling for emotional arousal of the animals. A combination of emotion indicators, along with preference tests could also help to validate the currently suggested vocal indicators of emotional valence found in farm animals. Finally, the indicators highlighted in this review should be validated by placing or observing the animals in novel experimental or natural positive and negative situations.

Table 6
The number of studies used in this review investigating the relationship between positive emotions and vocalisations categorised per farm animal species (search conducted up to October 2019, review articles were excluded). In the experimental studies, the animal itself or its environment is manipulated to measure the effect this has on the animal. In the observational studies, the animal is observed without manipulating the animal or its environment (Nordell and Valone, 2017). Underlined indicators supporting putative emotions are indicators suggested to be related to valence, based on evidence across species, including the cognitive bias, the RMSSD (root mean square of successive inter heartbeats interval differences) parameter of HRV (heart rate variability) and behavioural measurements (Paul et al., 2005; Kremer et al., 2020), including ear posture (Hall et al., 2018).

Species	Number of articles	Suggested a relationship between positive emotions and vocalisations	Number of animals per study	Indicators supporting the putative emotions	The positively and negatively valenced situations per study	Experimental research	Observational research
Pigs (including wild boars)	7	7	36 (Friel et al., 2019)	<u>Cognitive bias</u> HR (heart rate), HRV (SDNN, RMSSD and RMSSD/SDNN), behavioural measurements (e.g. exploratory and escape behaviour)	Food reward (positive), Provision of coffee beans, a food that is not liked (negative) Food reward, toy provisions, straw provisions (positive), various sounds and visual stimuli that aimed to startle the pig (negative)	6 (Imfeld-Mueller et al., 2011; Reimert et al., 2013; Leliveld et al., 2016; Riley et al., 2016; Briefer et al., 2019; Friel et al., 2019)	1 (Maigrot et al., 2018)
			32 (Briefer et al., 2019)	HR, HRV (RMSSD), behavioural measurements (e.g. freezing, escape and exploratory behaviour)	Being in a test arena with a conspecific, food and toys (positive); social isolation (negative)		
			24 (Reimert et al., 2013)	Salivary cortisol, behavioural measurements (e.g. freezing behaviour and play behaviour)	Provisions of straw, peat and chocolate raisins (positive); Social isolation and restraining the pig with a nose sling (negative)		
			16 (Imfeld-Mueller et al., 2011)	HR, HRV (RMSSD), locomotory activity	Provision of a food reward (positive); Crossing a ramp (negative)		
			8 (Riley et al., 2016)	None	The piglet was greeted (positive), The piglet was picked up (negative)		
Horses (including Przewalski's horses)	5	5	19 (Maigrot et al., 2018)	Body movement (indicator for arousal)	Food reward, affiliative interactions (positive), agonistic interactions (negative)		
			20 (Briefer et al., 2015a)	HR, HRV (RMSSD), respiration rate, skin temperature, behavioural measurements (e.g. ears, head and tail movements)	The reunion with one or more companions (positive); the removal of one or more companions (negative)		
			23 (Maigrot et al., 2017)	Body movement (indicator for arousal)	Food reward, affiliative interactions (positive); agonistic interactions, social separation (negative)	1 (Briefer et al., 2015a)	4 (Pond et al., 2010; Maigrot et al., 2017; Stomp et al., 2018a, b)
			20 (Stomp et al., 2018a)	<u>Ear position</u>	Observations in stall and pasture, no clear positive and negative situation is used		
			48 (Stomp et al., 2018b)	Stereotypes, ear position	Observations in stall and pasture, no clear positive and negative situation is used		
Cows	2	1 (Meen et al., 2015)	27 (Pond et al., 2010)	None	Feeding (positive), separation from foal (negative)		
			44 (Santos et al., 2019)	HR, respiration rate, rectal temperature, body surface temperature, behavioural measurements (e.g. movement and defecation)	During milking (no division between positive and negative valence)	0	2 (Meen et al., 2015; Santos et al., 2019)
Goats	1	1	141 (Meen et al., 2015)	Behavioural measurements (e.g. social interactions and play behaviour)	During feeding, lying & rumination, social interactions, stress, sexual behaviours and several other situations (no division between positive and negative valence)		
			22 (Briefer et al., 2015b)	HR, HRV (RMSSD), respiration rate, head movements, ear/tail posture	Food reward (positive); food frustration, social isolation (negative)	1 (Briefer et al., 2015b)	0 (continued on next page)

Table 6 (continued)

Species	Number of articles	Suggested a relationship between positive emotions and vocalisations	Number of animals per study	Indicators supporting the putative emotions	The positively and negatively valenced situations per study	Experimental research	Observational research
Sheep	1	0	27 (Tamioto et al., 2017) 12 (McGrath et al., 2017)	Ear posture and changes, half-closed eyes, tail wagging, body temperature	Brushing of the animal (positive)	1 (Tamioto et al., 2017)	0
Chickens	2	2	18 (Zimmerman et al., 2011)	None Behavioural measurements (e.g. wing flapping and preening)	Food reward, dustbathing reward (positive) Food reward (positive); spraying of water (negative)	2 (Zimmerman et al., 2011; McGrath et al., 2017)	0

6. Conclusion

In the present review we discussed the possible relationship between positive emotion and certain vocalisation types and parameters in a number of farm animal species. Measuring vocalisations can be applied in a continuous, non-invasive fashion and in a relatively easy way. However, with the current state of research, there is only enough evidence in pigs and some evidence in horses to suggest that vocalisations related to positive emotions can be identified. Therefore, more research combining natural observations and experimental manipulations is warranted to gather further evidence in other species, and to acquire stronger evidence in pigs and horses. Nevertheless, the small amount of research on cows, goats and chickens does predict a measurable relationship between positive emotions and vocalisations. Overall, vocalisations seem to be a good indicator of positive emotion, and when applied in combination with other indicators and tests, could be a promising on-farm tool to monitor positive emotions (McCloughlin et al., 2019).

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Declaration of Competing Interest

The authors report no declarations of interest.

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