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Unnecessary suffering during the slaughter of cattle and pigs: mapping stun quality and associations to stun-to-stick intervals

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Ensuring that animals remain unconscious and insensible until death occurs via blood loss is critical for animal welfare at slaughter. Two key factors are the rapid sticking procedure following stunning and a correct assessment of stunning efficiency. This observational study aimed to map and assess variations in stun quality among carbon dioxide (CO₂) stunned pigs and mechanically stunned cattle slaughtered under commercial conditions in Sweden. It also examined whether the duration of the stun-to-stick interval was associated with signs of consciousness. Data were collected between May 2023 and November 2024 across five pig slaughterhouses (n = 2,795 pigs) and six cattle slaughterhouses (n = 330 cattle). Stun quality was assessed based on established protocols and categorised as either good, doubt, shallow or poor. The primary findings revealed that longer stun-to-stick intervals were significantly associated with inadequate stun quality (i.e. shallow or poor stunning) and significantly increased the likelihood of re-stunning. In total, 96.1% of the pigs were adequately stunned. Notably, the proportion of pigs with inadequate stun quality ranged from 1.2 to 16.6% across slaughterhouses, with poor stunning observed in 0 to 9.1%. Restunning rates varied from 1.6 to 6.4%, and stun-to-stick intervals ranged from 32 to 199 s. For cattle, 92.7% of the animals were adequately stunned, with inadequate stunning ranging from 0 to 18.5%, poor stunning from 0 to 14.8%, re-stunning rates from 0 to 14.0%, and intervals between 77 and 192 s. The results indicated that intervals of less than 59 s for pigs and 99 s for cattle were associated with the lowest rates of inadequate stunning. Furthermore, the observed variation in stun quality among slaughterhouses highlights the potential for improvement in stunning practices, particularly in slaughterhouses with higher rates of stunning failures. Not all animals displaying symptoms of inadequate stunning were identified by the slaughterhouse personnel; instead, they continued along the

line, potentially conscious, which suggests critical gaps in monitoring. The correct use of stunning equipment, along with continuous training of personnel to accurately recognise signs of recovery, is crucial for protecting animals from unnecessary suffering throughout the slaughter process.

KEYWORDS

animal welfare, assessment, captive bolt stunning, cartridge, commercial slaughter, CO2 stunning, humane slaughter, pneumatic

1 Introduction

Humane slaughter of cattle (Bos taurus) and pigs (Sus scrofa domesticus) involves stunning followed by exsanguination, as mandated by Council Regulation (EC) No 1099/2009. Stunning is performed to induce unconsciousness and insensibility to pain, thereby ensuring that the animals avoid unnecessary distress prior to death (McKinstry and Anil, 2004; Terlouw et al., 2016). The subsequent exsanguination has two main objectives: to ensure death by inducing immense blood loss, and to ensure adequate meat quality. The interval between stunning and the initiation of bleeding should be kept as short as possible to prevent the risk of animals regaining consciousness and sensibility before brain death occurs due to blood loss, thereby minimising the risk of compromised animal welfare. Death is confirmed when both brain and cardiac functions have ceased (Jerlström, 2014), specifically when the respiratory and circulatory centres in the medulla oblongata are permanently inactive, and the brain is deprived of oxygen and nutrients (EFSA, 2004). Although definitions may vary, it is widely accepted that an unconscious animal is insensible and unable to perceive or respond to sensory stimuli, as its brain no longer processes sensory information (Blood and Studdert, 1988). As a result, it cannot experience pain or discomfort (Broom, 2022).

Slaughterhouses managed by Food Business Operators (FBOs) are profit-driven businesses that must maintain a consistent process flow of processed meat products according to the demands of the market, whilst simultaneously fulfilling consumer expectations for high animal welfare standards. Stunning prior to exsanguination is a crucial aspect of animal welfare at slaughter, and presents two primary challenges: 1) the potential for pain and fear during the stunning process itself, and 2) guaranteeing that the animal remains unconscious during the subsequent exsanguination procedures (Brandt and Aaslyng, 2015). The most commonly applied stunning methods for cattle and pigs in Europe include mechanical stunning with a penetrative captive bolt, electrical stunning by applying a current through the animal's head, and gas stunning, wherein animals are immersed in high carbon dioxide (CO₂) gas concentrations (EFSA, 2020a; 2020b). When performed correctly, mechanical stunning with a captive bolt results in irreversible unconsciousness, whereas electrical stunning is considered a reversible method, as the stunning effect will cease over time (EFSA, 2004). In gas stunning, the potential for irreversible stunning is related to the gas concentration and the duration of gas exposure. Stunning procedures are complex and present several challenges, as animal welfare, worker safety, product quality, and economic considerations (Jerlström et al., 2022) must all be contemplated.

Through the CO_2 stunning method, animals are exposed to an environment with high concentrations of CO_2 . Following Council Regulation (EC) 1099/2009, a minimum of 80% CO_2 must be used, and the pigs must remain exposed for a duration long enough to render them unconscious. The effectiveness of CO_2 -stunning in preventing animal suffering is dependent on several factors: exposure time, CO_2 concentration, the interval between stunning and sticking, and the efficiency of bleeding. The physiological principle of CO_2 -stunning involves a combination of the acidification of brain cells and acute hypercapnia (high concentrations of CO_2), leading to a reduction in brain activity, decreased awareness, and ultimately unconsciousness or death (Rodríguez et al., 2008; Llonch et al., 2012; Atkinson et al., 2020). Higher CO_2 concentrations reduce the time required to achieve unconsciousness and/or death (Terlouw et al., 2016).

The principle of captive bolt stunning is to induce an immediate and irreversible loss of consciousness and sensibility in animals with a single shot. This method, frequently used among cattle, utilises a captive bolt device, usually a retractable rod, which penetrates the skull and causes substantial physical damage to the brain. Unconsciousness is achieved through shock waves generated by the bolt, which damages brain tissue, disrupts cerebral blood flow, and impairs neuronal function (Kamenik et al., 2019). The impact of the bolt specifically targets vital areas of the brain, disrupting cortical activity and increasing intracranial pressure, resulting in an immediate loss of consciousness (Terlouw et al., 2016; Terlouw and Le Neindre, 2024).

Within the EU, each FBO should define the maximum stun-to-stick intervals applicable at each separate slaughterhouse in their standard operating procedures (SOPs) (Council Regulation (EC) 1099/2009, 200), with the starting point being the generally accepted maximum duration of 60 s for pigs stunned with CO₂ gas and cattle stunned mechanically (Holst, 2001; EFSA, 2004; European Commission, 2017). However, many slaughterhouses struggle to meet this standard due to the technical design of their

systems, including the layout of the shackle line and the slaughter process speed. When mechanical stunning and sticking procedures are performed correctly, extended stun-to-stick intervals (i.e., longer than 60 s) do not necessarily risk animal welfare (Atkinson and Algers, 2007). However, only a few studies have focused on how stun quality is affected by increased stun-to-stick intervals, possibly because of the ethical and practical challenges of conducting such research.

To regularly monitor and evaluate indicators of consciousness, unconsciousness, and the risk of recovery, it is essential to ensure that animals do not display signs of sensibility from the end of the stunning process until death (Council Regulation (EC) 1099/2009). Such monitoring (Gregory and Shaw, 2000) is vital to prevent unnecessary suffering, including pain, distress, or prolonged discomfort caused by ineffective stunning. Stun quality assessment includes verification that equipment and stunning methods are effective and close observation of physical signs such as behavioural indicators related to consciousness or residual brain function (Levitis et al., 2009). If there are indications that an animal is inadequately stunned, or that the animal is about to regain consciousness or sensibility, immediate and rapid corrective measures, such as restunning, must be taken without delay (Verhoeven et al., 2014; SJVFS, 2019:8; Algers and Berg, 2022; Terlouw and Le Neindre, 2024).

Gregory et al. (1987); EFSA (2020a; 2020b), and Welfare Quality [®] (2009) provide guidelines for assessing stun quality, including indicators such as an absence of corneal reflex, righting reflex, rhythmic breathing, and vocalisations. Other useful indicators include eyeball rotation, pain responses (e.g., pricking the snout or muzzle), and spontaneous blinking (EFSA, 2004; 2013a; 2013b; Grandin, 2013). However, certain indicators, e.g., gasping in pigs, defined as short, abrupt gasps of air, leave room for interpretation. Atkinson et al. (2012) demonstrated that gasping is an important indicator of insufficient stunning in pigs, and that the most frequent combination of symptoms was corneal reflex and regular gasping. Other studies consider gasping to be more of a rudimentary brainstem reflex (Raj, 1999) and a symptom of the dying process (Grandin, 2010).

In a Swedish study where stun quality was assessed among 998 cattle, most animals were stuck between 84 and 125 s after stunning. In total, 84.1% were adequately stunned, 12.5% were inadequately stunned, and 3.3% were categorised with an uncertain stun quality (Atkinson et al., 2013). A similar study examining 9,520 pigs revealed that slaughterhouses using a paternoster CO₂ gas stunning system generated a better stun quality compared to those using dip-lift systems (99.9% compared with 98.2%), and that stun-to-stick intervals reaching up to 100 s, when pigs were stunned in paternoster systems, did not risk animal welfare (Atkinson et al., 2012). However, the stun-to-stick interval must be adjusted according to the technical parameters (e.g., gas concentration or suitable cartridge strength) of the stunning method and its efficacy (EFSA, 2020a; 2020b).

Against this background, this study aimed to map and assess variations in stun quality in CO₂-stunned pigs and mechanically

stunned cattle under commercial slaughter conditions. It also aimed to examine how prolonged stun-to-stick intervals may be associated with an increased risk of animals regaining consciousness, potentially leading to unnecessary suffering and compromised welfare.

2 Materials and methods

This observational study was conducted with the approval of the Swedish Animal Research Ethics Committee in Gothenburg in compliance with Swedish regulations (SJVFS 2019/9). In total, 2,795 finishing pigs from seven slaughterhouse visits (five slaughterhouses, with two necessary additional visits) and 330 cattle from six slaughterhouse visits (six slaughterhouses) were assessed between May 2023 and November 2024. The assessments were conducted at medium- and large-scale slaughter facilities (ranging from approximately 300-1,700 pigs or 31-210 cattle slaughtered per day) during routine slaughter operations. The number of animals assessed on each observation day varied depending on the slaughter speed and capacity of the facility, ranging between 17 and 93% of pigs and 8 and 94% of cattle slaughtered at the facility on the observation day. Observations were carried out for one to three days per slaughterhouse, but not always on consecutive days. The same observer with extensive experience in animal welfare at slaughter and expertise in evaluating stunning effectiveness performed all assessments. During each assessment round, the stun-to-stick interval, along with the clinical signs of unconsciousness and consciousness exhibited by the animals after stunning, were recorded. Only limited information on the involved slaughter facilities could be provided to maintain confidentiality.

2.1 Pigs

A total of 2,795 finishing pigs reared in commercial herds of halothane-negative hybrids of commercial breeds (originating from Topig Norsvin, Danavl, Scan Sverige) were assessed during routine stunning at five slaughterhouses with medium to large-scale processing rates. In accordance with EU legislation, the slaughterhouses used a standard stunning method involving a combination of gas concentration and exposure time that did not cause immediate death; thus, the pigs were ultimately killed by exsanguination. Three slaughterhouses were assessed once, whilst two were assessed on two occasions, following adjustments in CO₂stunning parameters and slaughter routines. Recording at each assessment lasted between one to two days. In Sweden, finishing pigs are typically slaughtered at around five to six months of age, at a live weight of 120 kg. Pigs were stunned in groups, with different people operating the shackling and sticking, usually one person at each station. The total number of observations from each assessment occasion was as follows: 513, 168, 184, 379, 503, 513, and 514.

2.1.1 Stunning procedure and system settings

At each of the involved slaughterhouses, groups of pigs were placed within a cage that was lowered into a CO₂-filled pit. Two primary systems were used: the dip-lift system and the paternoster system. In the dip-lift system, a cage containing up to eight pigs was lowered into a pit at a depth of two to four metres, where pigs were exposed to the highest CO₂ concentration at the bottom, as CO₂ is a heavy gas (Figure 1). In the paternoster system, up to seven rotating cages, each carrying two to seven pigs depending on the model, moved through a CO₂ gradient in a pit three to eight metres deep (Figure 2). Live pigs were loaded at one end of the system, whilst unconscious pigs were unloaded for sticking at the other end. In this study, three slaughterhouses used the Butina[®] paternoster stunning system, and two used the Butina[®] dip-lift stunning system.

The CO₂ stunning systems included in this observational study operated under different gas concentrations, temperatures, and durations. Each slaughterhouse had adjusted parameters such as the number of pigs per cage, the time required to reach peak CO₂ levels, temperature, and the total exposure time based on operational requirements and the FBOs SOPs. These parameters were digitally recorded within the system, as regulated by EU Regulation 1099/2009, and provided to the research team by the FBO after each occasion. Group sizes in the cages were recorded by counting the number of pigs in each group as they fell out of the cage but are not presented here to maintain confidentiality. Data on CO₂ concentration and temperature were collected on 11 of 13 observation days, and exposure time data were collected on seven of 13 observation days. At one slaughterhouse, the system did not record CO₂ temperature, but this was resolved by installing a

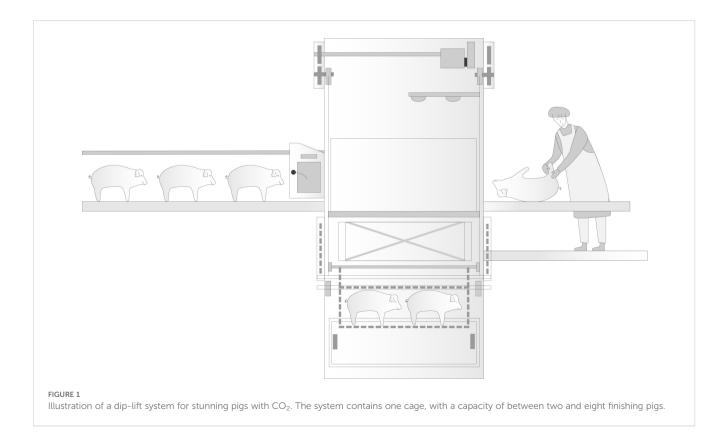
portable temperature meter. Furthermore, double-edged sticking knives with blade lengths ranging from 16 to 21 cm were used in all five slaughterhouses.

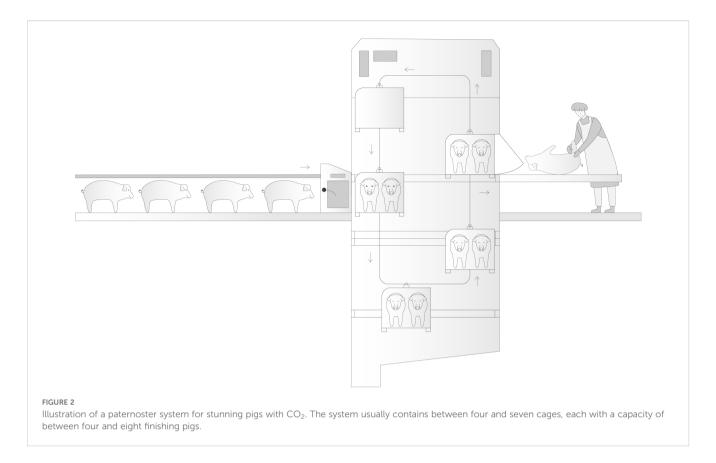
2.1.2 Stun-to-stick intervals

Stun-to-stick intervals were recorded individually using a stopwatch. Due to practical reasons, recordings were performed on only the last four pigs if the group size reached seven or eight. Stunning ceased when the cage stopped just before the gate was opened to empty the pigs onto the shackling table. In addition, the FBOs measured where the pigs passed the level of less than 80% $\rm CO_2$ concentration, and this interval was added to the total stunstick time. Among all pigs, bleeding was initiated through chest sticking, a procedure that involves severing major thoracic blood vessels (Figure 3). The time point at which the knife was inserted into the chest was used to define the end of the stun-to-stick interval.

2.1.3 Stun quality assessment

Stun quality was assessed by observing pigs for physical symptoms indicative of consciousness or risk of recovery from unconsciousness, following protocols developed in previous studies by Atkinson et al. (2012). These protocols have been proven as reliable and effective in identifying inadequate stun quality, using a five-level classification system. However, in the present study, the levels were modified to four levels, designated as "good", "doubt", "shallow", and "poor" (Table 1). For statistical analysis, the stun quality levels were further pooled. Stun quality level 1 categorised deviations in stun quality into two classes: (1) good and doubt, and





(2) shallow and poor. Stun quality level 2 targeted severe deviations, which also had two classes: (1) good, doubt, and shallow, and (2) poor (Table 2).

The corneal reflex, tested by carefully touching the corneal area of the eye with a fingertip, was intended to be tested on all pigs prior to sticking. However, this was not feasible for all animals. If pigs displayed symptoms of ineffective stunning, the corneal reflex was tested again, when possible. A blink response (fast or slow) was recorded as a positive corneal reflex. The pain reflex was assessed on a randomised subset of animals, typically all observed pigs in every fifth or sixth group of stunned pigs, depending on group size, by pricking the snout with the sharp point of a metal stick. A withdrawal response was recorded as a positive pain reflex. Stun quality was continuously assessed until two minutes after sticking. If the group size was seven or eight, observations were performed on the last four pigs in the group due to practical reasons.

2.2 Cattle

A total of 330 cattle were observed during routine stunning procedures at six Swedish slaughterhouses with medium- to large-scale processing capacities, over one to three days per site. At these slaughterhouses, observations were made on 38, 44, 57, 60, 62, and 69 cattle, respectively. The examined animals consisted of 183 females (125 cows and 58 heifers) and 147 males (114 young and mature bulls and 33 steers). The animals were further categorised into dairy breeds and beef and/or crossbreeds, with a distribution of

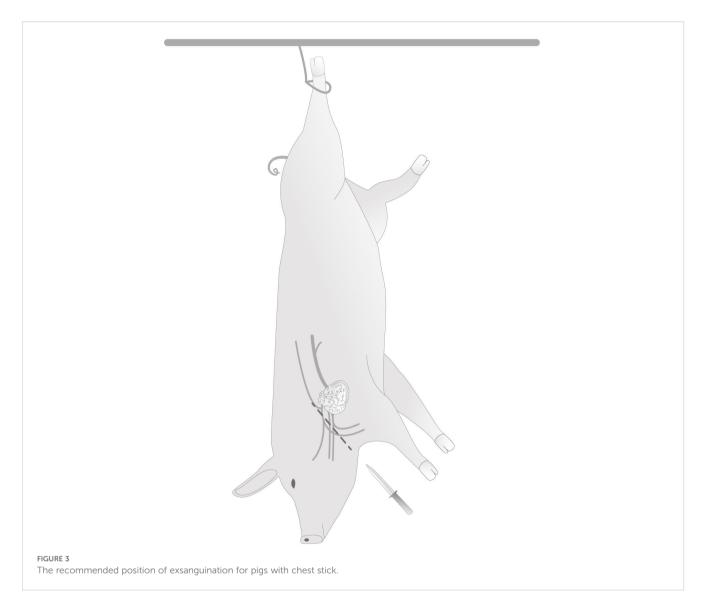
47.0% dairy breeds and 53.0% beef and/or crossbreeds. Information regarding age and carcass weight of the selected animals was obtained from the FBOs, but the sex and breed type were registered at the time of slaughter (Table 3).

2.2.1 Stunning procedure

Cattle were stunned individually in stun boxes with or without head restraint equipment. The shooter was generally not the same person who shackled and bled the animal, but this varied between FBOs. There were two types of pneumatic stunners and six types of cartridge-driven captive bolts (varying in calibre, bolt velocity, kinetic energy, bolt length, and diameter) used in the observed stunning events in this study. Five of the cartridge-driven captive bolts were.25 calibre, and one was.27 calibre. The length of these bolts varied between 65-95 mm, and the diameter ranged from 11.4 to 12 mm. The bolts of the two pneumatic stunners were 85 mm long, with diameters of 15.2 and 15.9 mm. Gun type was nested within the slaughterhouse, together with sample sizes that were too small for each gun type; therefore, no further statistical analysis of gun type effects was performed. Furthermore, the types of knives used for bleeding varied among the slaughterhouses. Single-edged sticking knives were used in four of the six slaughterhouses, with blade lengths ranging from 14.5 to 21 cm.

2.2.2 Shot accuracy

The application spot of the gun (shot accuracy and angle) was recorded on each animal's skull following decapitation. Proper shot precision is ensured by targeting the point where two imaginary



lines, drawn from the base of the horns to the opposite eye, intersect (Figure 4). The shot should occur no more than two cm from this ideal point (EFSA, 2004). If the shot hole was more than two cm outside the target area in any direction, it was considered inaccurate. If the angle of the shot deviated more than 20 degrees from the recommended perpendicular angle to the skull bone, it was recorded as a deviated angle (Figure 5).

2.2.3 Stun-to-stick intervals

The stun-to-stick interval was recorded using a stopwatch, timed from when the shot was heard or seen to when the knife was inserted into the chest to sever the large blood vessels in the thoracic cavity (Figure 6). Registrations were made on the type of cattle shot, i.e., dairy, beef, or crossbreed; sex (young bull, mature bull, cow, heifer, steer), the number of times the animal was shot, and the duration of the shots and re-shots. The type of captive bolt used (pneumatic or cartridge-driven) was also documented, with technical parameters provided by the FBOs, as well as the type of knives used for exsanguination.

2.2.4 Stun quality assessment

Signs of successful stunning include motor paralysis and immediate collapse within the stunning box, with no observable signs of corneal reflex, response to painful stimuli, attempts to regain an upright posture, vocalisation, or rhythmic breathing (Atkinson et al., 2013; EFSA, 2013a; 2013b; Grandin, 2013; Večerek et al., 2021). Additional indicators, such as tongue tension, could be used as complementary measures but cannot be relied upon as sole indicators of unconsciousness (Von Holleben et al., 2010).

Based on a stun quality protocol developed by Atkinson et al. (2013), stun quality was assessed and categorised into stun quality levels from the time of stunning until two minutes after sticking (Table 4). The protocol used in Atkinson's study was proven to be both feasible and effective in differentiating animals that exhibit high-risk signs of recovery and compromised animal welfare from those in moderate- and low-risk categories, using four levels of stun quality. In this study, we refer to the different levels as good, doubt, shallow, and poor. For statistical analysis, the stun quality levels

TABLE 1 Criteria used to classify the stun quality of $\rm CO_2$ stunning of pigs from stunning until two minutes after sticking (summarised from Atkinson et al., 2012).

Stun quality	Criteria	Examples of signs	
Good	The animal is in a state of deep unconsciousness and adequately stunned, and there is no risk of poor animal welfare.	No evidence of rhythmic breathing, righting reflex, vocalisation, convulsion, blinking and/or eye responses to stimulation.	
Doubt	If shown, the animal is considered adequately stunned but requires continual monitoring.	Irregular kicks (or other movements), irregular gasps, but no eye reflexes.	
Shallow	The stun depth is considered unacceptable due to the risk that the animal could recover. Restunning is necessary as a precaution to avoid recovery of consciousness.	Regular gasps, kicks, or body convulsions, but no eye reflexes.	
Poor	The stun depth is inadequate, and the recovery risk is considered imminent. The criteria indicate some form of consciousness and a high risk for poor welfare. Immediate re-stunning is necessary.	Positive corneal reflex at sticking, with or without kicking or convulsions, spontaneous blinking, righting reflex, vocalisation, and/or positive pain reflex.	

were further pooled in the same manner described for the pigs (Table 5).

A similar assessment to the one described for pigs involving the testing of corneal and pain reflexes was conducted on cattle. However, the selection of animals for the pain reflex test was based on how they landed after exiting the stun box; specifically, animals that had their heads positioned against the stun box were not tested, as it was not practically feasible to access them safely in that position.

2.3 Statistical analysis

Data editing and descriptive statistical analyses were performed with Excel 2016 (Microsoft Corp., Redmond, Washington, DC, USA). Statistical analyses were conducted using SAS Software (version 9.4 of the SAS system, SAS Institute Inc., Cary, NC, USA). The statistical unit for analysis was the individual animal

(cattle or pigs). For cattle, a total of 309 observations (stun quality 1 and 2) and 315 observations (for the occurrence of re-stunning) were included in the statistical analysis. The corresponding observations for pigs were 2,775. Exclusion of observations was due to incompleteness.

Effects of stun to stick interval on the pooled categories stun quality 1 [good/doubt vs. shallow/poor], stun quality 2 [good/doubt/shallow vs. poor], and the occurrence of re-stunning [yes vs. no] was assessed with generalised linear models using the GLIMMIX procedure in SAS, applying a binomial distribution and a logit link function. Models were developed using a stepwise-backward selection of predictor effects, where non-significant effects and interactions were removed from the model. The final models for pigs (model 1) and cattle (model 2) are presented below.

Model 1:

y = Stun - to - stick interval + Type of stunning system

- + Slaughterhouse visit (Type of stunning system)
- + Observation day + e

where y is the binomial response variable being assessed (stun quality 1, stun quality 2, re-stunning), the stun-to-stick interval (s) was included as a covariate, and the type of stunning system (Paternoster/Dip-lift, 2 classes), slaughterhouse visit nested within stunning system (1-7, 7 classes), and observation day (1/2, 2 classes) included as fixed control class effects, and e represents a random error term to account for unexplained variability. Observation day was included to account for variations between different observation days.

Model 2:

y = Stun - to - stick interval + Age + Slaughterhouse visit+ Shot accuracy + Sex + Breed type + e

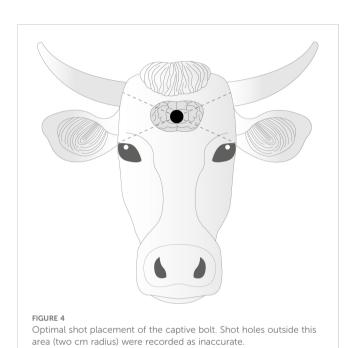
where y is the binomial response variable assessed (stun quality 1, stun quality 2, re-stunning), the stun-to-stick interval (s) and age were included as covariates, and slaughterhouse visit (1-6, 6 classes), shot accuracy (Yes/No, 2 classes), sex (Female [cow and heifer]/ Male [young bull, mature bull, steer], 2 classes), and breed type (Dairy/Beef [beef and crossbreed], 2 classes) included as fixed class control effects, and e represents a random error term to account for unexplained variability.

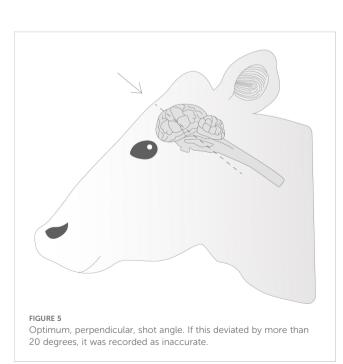
TABLE 2 Distribution across the four levels of stun quality, frequency of re-stunning, and the pooled categories stun quality 1 and 2, in pig observations.

Stun quality	Number of animals (%)	Number of re-stuns (%)	Stun quality 1 (deviations in stun quality)	Stun quality 2 (severe deviations in stun quality)
Good	2,647 (94.7)	2 (1.8)	2 (0(1)	2,753 (98.5)
Doubt	39 (1.4)	12 (10.6)	2,686 (96.1)	
Shallow	67 (2.4)	58 (51.3)	100 (2.0)	
Poor	42 (1.5)	41 (36.2)	109 (3.9)	42 (1.5)
Total	2,795	113 (4.0)	2,795	2,795

TABLE 3 Distribution of carcass weight (kg) and age (months) among the studied animals.

Cattle category	N	Mean (± SD) carcass weight (kg)	Range (kg)	Mean (± SD) age (months)	Range (months)
Cows and heifers	183	314 (± 68.7)	166-514	51 (± 30.4)	13-175
Bulls (both young and mature)	114	353 (± 72.2)	240-643	20 (± 15.3)	11-128
Steers	33	337 (± 49.5)	240-415	25 (± 3.8)	18-34





3 Results

3.1 Pigs

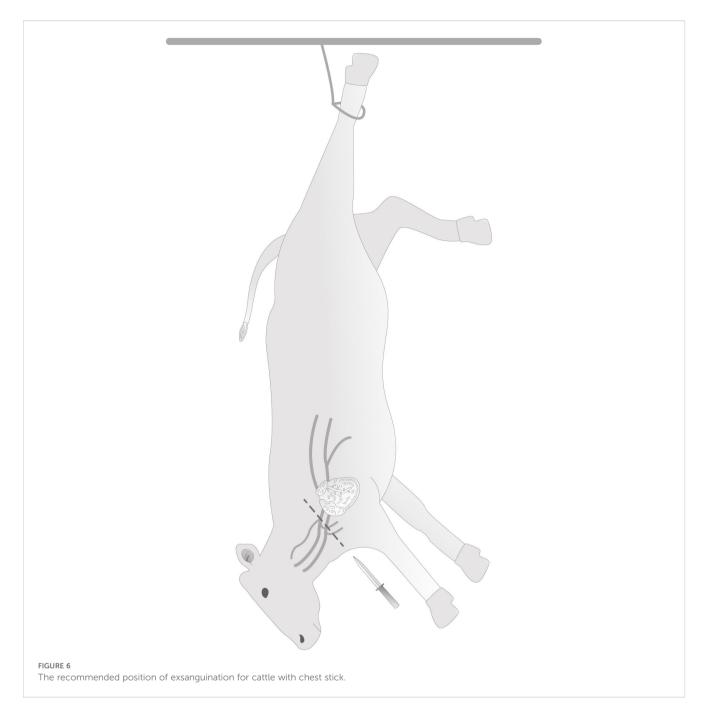
In the groups of observed pigs, the group size within the stunning system ranged from four to eight (5.3 \pm 1.6). The CO₂ concentration settings ranged from 89 to 94%, and the minimum and maximum values of the actual CO2 concentration on the observation days ranged from 85 to 92.9% and 87 to 95.1%, respectively. On 11 of 13 observation days, the actual CO2 concentrations were below the system's set points, with five slaughterhouses containing average CO2 concentrations below their respective set points. According to the SOPs of three slaughterhouses, the temperature settings should be between 15 and 20°C, and for two slaughterhouses, the range should be between 15 and 25°C. The observed CO₂ temperatures ranged from 14.1 to 25.2°C, and 15.6 to 25.2°C, respectively, on the days of observation, with actual temperatures falling below the set levels on one day of observation and exceeding them on three days of observation. Exposure times to CO₂ concentrations greater than 80% were set between 140 and 169 s. The average actual exposure times during the observation days ranged from 151.5 to 190 s and 150 to 183 s, respectively.

3.1.1 Stun-to-stick intervals

The average stun-to-stick interval was 90 s (\pm 21.5 SD), ranging from 32 to 199 s (Q1 = 74, Q3 = 107 s). A total of 113 pigs (4.0%) were re-stunned. Most of the animals, 1,760 (63.0%), were stunned in the paternoster systems, whilst 1,035 (37.0%) were stunned in the dip-lift system.

3.1.2 Stun quality and the impact of stun-to-stick intervals on stun quality

Of the 2,795 pigs, 96.1% were adequately stunned, i.e. there were no deviations in stun quality. Inadequate stunning was observed among 3.9% of the animals, with 2.4% displaying signs of shallow stunning and 1.5% showing symptoms of poor stun quality (Table 2). The percentage of pigs demonstrating deviations in stun quality (stun quality 1) varied between slaughterhouses, ranging from 1.2 to 16.6%. Severe deviations in stun quality (stun quality 2) ranged from 0 to 9.1%. Additionally, the percentage of pigs that were re-stunned varied between slaughterhouses from 1.6 to 6.4%.



Corneal reflex was tested on a total of 2,767 pigs (missing 28 observations) either before or in close connection to sticking. Pain reflex was assessed on a subset of pigs, typically every fifth or sixth group of stunned pigs, depending on group size and slaughter process speed, resulting in a total of 1,093 pigs (missing 1,702 observations), with one (0.1%) having a positive response.

The two most frequently observed indicators of inadequate stun quality were regular gasping (n=104, 3.72%) and positive corneal reflex (n=42, 1.52%). Other observed indicators included irregular gasping (n=33, 1.18%), irregular kicking (n=11, 0.39%), regular kicking (n=2, 0.07%), rhythmic breathing (n=1, 0.04%), and convulsions (n=1, 0.04%). Vocalisation, spontaneous blinking, nystagmus, eyeball rotation, and righting reflex were never

observed throughout the study. Further, a positive corneal reflex was detected in 37 (35.56%) of the pigs that demonstrated regular gasping and six (18.18%) with irregular gasping.

3.1.2.1 Impact of stun-to-stick intervals on stun quality and re-stunning

The stun-to-stick interval had a significant effect on deviations in stun quality (stun quality 1: b=0.046, F=57.52, p<0.001), indicating that increased intervals are related to an increased proportion of pigs with shallow or poor stun quality. There was also a significant effect of stun-to-stick interval on the proportion of pigs with severe deviations in stun quality, i.e., poorly stunned (stun quality 2: b=0.053, F=29.32, p<0.001). Additionally, the stun-to-

TABLE 4 Criteria used to classify the stun quality of captive-bolt stunning of cattle from stunning until two minutes after sticking (summarised from Atkinson et al., 2013).

Stun quality	Criteria	Examples of signs
Good	The animal is deeply stunned, and there is no concern of recovery or reduced animal welfare.	Immediate collapse, no attempt to get up, eyes open and not moving, pupils completely dilated.
Doubt	If shown, the animal is considered adequately stunned but closely monitored and tested for reflexes.	The tongue is retained in the mouth, excessive kicking with the limbs that produces a danger to the operator.
Shallow	Inadequately stunned, but with a moderate recovery risk and compromised animal welfare. Re-stunning is necessary to eliminate recovery risk.	Nystagmus, characterised by side- to-side eye movements, eyeball rotation where the sclera is predominantly visible with minimal or no iris observed 40 s after stunning, gasping for air.
Poor	Inadequately stunned, with the highest risk of recovery and compromised animal welfare. Immediate re- stunning is required to prevent suffering.	No collapse, rhythmic breathing, positive corneal reflex, positive pain reflex (if possible to assess), spontaneous blinking, vocalisation.

stick interval had a significant effect on the proportion of re-stunned pigs (b=0.045, F=56.90, p<0.001), indicating that an increased stunto-stick interval is related to a higher likelihood of restunning (Figure 7).

3.1.2.2 Impact of control factors on stun quality and restunning

The type of stunning system significantly affected the proportion of pigs with observed deviations in stun quality (F=59.40, p<0.001), indicating that a higher proportion of pigs stunned in paternoster systems had shallow or poor stun quality compared to those stunned in dip-lift systems. There was no significant effect regarding the type of stunning system used on the proportion of pigs with severe deviations in stun quality, i.e., poor stun quality. However, the type of stunning system had a significant effect on the proportion of pigs that were re-stunned (F=53.70, p<0.001), indicating that a higher proportion of pigs stunned in paternoster systems were re-stunned, compared to pigs stunned in a dip-lift system.

3.2 Cattle

3.2.1 Shot accuracy

Inaccurate shots, i.e., shots outside the target area (Figure 4), occurred in 74 (23.4%) of the observations (N=316). Of these, 11 animals were re-shot. Eight of the animals that were accurately shot (n=242) were re-shot. In total, 16 of the accurately shot cattle were inadequately or shallowly stunned. Inaccurately shot cattle were inadequately or shallowly stunned in seven of the observations. Shots below the target area were more common than shots above the target area (76.4% vs. 15.3%), with 8.3% of shots placed to the right or left.

Deviation in shooting angle (i.e., more than 20 degrees from the recommendation of 90 degrees, Figure 4) occurred in 78 (22.8%) of cattle (N=325). Of these, 10 animals were re-shot. Of the cattle shot with a correct shooting angle (n=247), six animals were re-shot. Three of the re-shot animals' skull observations could not be completed.

3.2.2 Stun-to-stick intervals

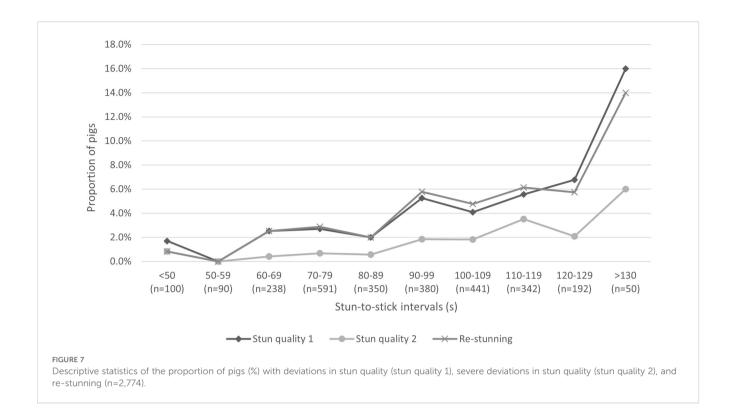
The average stun-to-stick interval was 106 s (\pm 15.6 SD), ranging from 77 to 192 s (Q1 = 90, Q3 = 118 s). A total of 19 cattle (5.6%) were re-shot. Most of the animals, 232 (70.3%), were stunned with cartridge-driven captive bolts, whilst 98 (29.7%) were stunned with pneumatically powered penetrating captive bolt guns. Among the 19 re-stunned animals, 16 were initially shot with cartridge-driven captive bolts, and three with pneumatic stunners.

3.2.3 Stun quality and the impact of stun-to-stick intervals on stun quality

Of the 330 cattle, 92.7% were adequately stunned. Among these, 31.9% exhibited doubtful symptoms, such as tongue tension or intense kicking in response to shackling or sticking. Shallow or poor stunning (stun quality 1) was observed in 7.3% of the animals, with 1.8% displaying signs of shallow stunning and 5.6% showing symptoms of poor stunning (Table 5). The percentage of animals demonstrating inadequate stun quality (stun quality 1) varied between slaughterhouses, ranging from 0 to 18.5%. The proportion of animals with severe deviations in stun quality, i.e. poor stun quality (stun quality 2) ranged from 0 to 14.8%. Additionally, the percentage of animals that were re-stunned varied between slaughterhouses ranging from 0 to 14.0%.

TABLE 5 Distribution across the four levels of stun quality, frequency of re-shots, and the pooled categories stun quality 1 and 2, in observations of cattle.

Stun quality	Number of animals (%)	Number of re-shots (%)	Stun quality 1 (deviations in stun quality)	Stun quality 2 (severe deviations in stun quality)
Good	201 (60.8)	6 (31.6)	306 (92.7)	
Doubt	105 (31.9)	2 (10.5)	300 (92.7)	312 (94.5)
Shallow	6 (1.8)	2 (10.5)	24 (7.2)	
Poor	18 (5.6)	9 (47.4)	24 (7.3)	18 (5.5)
Total	330	19 (5.6)	330	330



Of the 144 male cattle, 12 out of 106 young bulls, one out of six mature bulls, and three out of 32 steers exhibited symptoms of inadequate stun quality, compared to the 179 female cattle, where the corresponding numbers were five out of 122 cows and one out of 57 heifers. In total, 16 of 144 (11.1%) male cattle and six of 179 (3.4%) female cattle showed symptoms of inadequate stun quality. Seven observations were missing due to incomplete registrations.

The two most frequently observed indicators within the stun quality category doubt were tongue tension (n=92, 28.13%) and excessive kicking in response to shackling or bleeding (n=36, 10.94%). Other observed indicators included righting reflex (n=12, 3.65%), eyeball rotation (n=7, 2.12%), positive corneal reflex (n=5, 1.52%), no loss of the standing posture (n=4, 1.21%), rhythmic breathing (n=4, 1.21%), blinking (n=2, 0.61%), and nystagmus (n=1, 0.30%). Vocalisation was never observed. Pain reflex was assessed in 77 cattle, all of which produced a negative response. The corneal reflex was tested on all animals before or in connection with sticking.

3.2.3.1 Impact of stun-to-stick intervals on stun quality and re-stunning

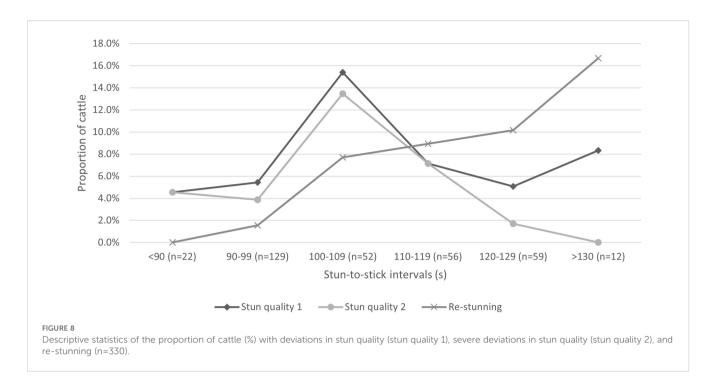
The stun-to-stick interval had a significant effect on the proportion of cattle with deviations in stun quality (stun quality 1: b=0.035, F=4.00, p=0.047), indicating that increased intervals are related to a slight increase in the proportion of cattle with shallow or poor stun quality. There was no significant effect of stun-to-stick interval on the proportion of cattle with severe deviations in stun quality. Moreover, the stun-to-stick interval had a significant effect on the proportion of re-shot cattle (b=0.050, F=6.53, p=0.011), indicating that an increased stun-to-stick interval is related to a higher proportion of re-stunned cattle (Figure 8).

3.2.3.2 Impact of control factors on stun quality and restunning

There was no significant effect of inaccurate shot placement on either the proportion of cattle with deviations in stun quality, i.e., shallow or poor stun quality, or the proportion of cattle with severe deviations in stun quality, i.e., poor stun quality. However, shot accuracy had a significant effect on the likelihood of cattle being restunned (F=7.64, p=0.006), indicating that a shot placed outside the optimal shot placement increased the proportion of re-stunned cattle, compared to a shot in the optimal target area. The sex of the animal (cow/heifer or bull/steer) had a significant effect on the proportion of cattle with deviations in stun quality (stun quality 1: F=6.39, p=0.012) and severe deviations in stun quality (stun quality 2: F=4.05, p=0.045), indicating that a higher proportion of bulls and steers were inadequately stunned compared to cows and heifers. However, sex had no significant effect on the likelihood of cattle being re-stunned. Furthermore, the breed of the animal (dairy or beef/crossbreed) did not have a significant effect on the proportion of cattle with deviations in stun quality, severe deviations in stun quality, or the likelihood of being re-stunned.

4 Discussion

The purpose of pre-slaughter stunning is to induce unconsciousness, thereby minimising pain and distress throughout the slaughter process (McKinstry and Anil, 2004). Guidelines have been established to assess the effectiveness of stunning (EFSA, 2020a; 2020b) with the aim of reducing unnecessary suffering at slaughter. In this study, we mapped and assessed variations in stun quality across five pig slaughterhouses,



two of which were visited twice (n = 2,795), and six cattle slaughterhouses (n = 330) in Sweden. We also sought to examine whether the duration of the stun-to-stick interval was associated with animals showing signs of consciousness during slaughter.

Our findings show that longer duration in the stun-to-stick intervals increased the risk of inadequate stunning, i.e., deviations in stun quality, in both CO2-stunned pigs and mechanically stunned cattle. For pigs, the highest proportion of adequately stunned pigs, i.e., those without deviations in stun quality, was when the sticking time was between 50 and 59 s, whilst the highest proportion of inadequately stunned pigs, i.e., those with deviations in stun quality, occurred when the time to bleeding exceeded 130 s. Interestingly, stun-to-stick intervals of 90 to 99 s resulted in nearly double proportions of pigs with deviations in stun quality (shallow or poor) compared to 60 to 69 s intervals, supporting current recommendations to bleed pigs within 60 s (Figure 7). Regarding cattle, the proportion of animals with inadequate stun quality distinctly increased as the time between stunning and sticking increased. The highest proportion of adequately stunned cattle was found when sticking occurred within less than 90 s, whilst the proportion of inadequately stunned animals peaked between 100 and 109 s. A near-linear increase in the likelihood of re-stunning was observed as the time to sticking increased (Figure 8). This may indicate that increased intervals provide operators more time to assess animals, potentially increasing both caution and uncertainty in interpreting symptoms of poor stun quality. Additionally, we observed inconsistencies in re-stunning practices, as some cattle showing signs of inadequate stun quality were not re-stunned, particularly when the stun-to-stick interval was below 110 s. Conversely, certain animals lacking any clear signs of inadequate stunning were re-stunned, notably when stun-to-stick intervals exceeded 110 s. This inconsistency suggests a lack of standardised assessment criteria (and implemented SOPs) among slaughter personnel, highlighting the need for clearer guidelines,

more elaborate SOPs, improved compliance with these, and improved and possibly repeated training (EFSA, 2020a; 2020b). Also, in the context of animal welfare, it is important to note that even when re-stunning is carried out promptly, animals may have already regained partial consciousness, thus been exposed to pain or distress (Terlouw et al., 2016), before re-stunning occurs.

4.1 Stunning efficiency for pigs

Among pigs, the results indicate that, on average, 3.9% of the animals showed signs of shallow or poor stunning, with 1.5% of pigs classified with poor stun quality, implying a high risk of recovery from unconsciousness or insufficient stun quality from the beginning. The variation in the proportion of poorly stunned pigs across the seven slaughterhouse visits ranged from 1.2 to 16.6%, including the two slaughterhouses that required additional visits due to equipment failures and issues with the implementation of SOPs. Although EFSA (2004) considered up to 5% of pigs with corneal reflex at the time of sticking to be acceptable, more recent research suggests that this threshold may be too high. Indeed, von Wenzlawowicz et al. (2012) reported a substantial variation in stunning effectiveness across slaughterhouses, and similar to our study's findings, they reported 1.8% of pigs with insufficient stunning, a finding consistent with Atkinson et al. (2012), who observed positive corneal reflex in 2.6% of pigs. Relying solely on fixed thresholds imposes risks of overlooking important contextual factors. A more comprehensive assessment would be more appropriate, including the competence of management and personnel in the implementation of SOPs, and their ability to operate and monitor stunning equipment. The assessment should evaluate personnel competence and responsiveness to deviations in stun quality, as well as faults in stunning equipment function

(EFSA, 2020a; 2020b). Such an integrated approach is essential to ensure high animal welfare standards.

We observed a significantly higher proportion of inadequately stunned pigs in slaughterhouses that use paternoster systems compared to dip-lift systems. This contrasts with Atkinson et al. (2012), possibly due to factors not recorded at the individual pig level and thus not accounted for in the present study, such as gas concentration and gas exposure time. However, since 2012, the carcass weight of finishing pigs has increased by 12% in Sweden (WinPig, 2024), and it is possible that slaughterhouses have not considered this when adjusting the capacity of individual cages. A major issue that significantly affects animal welfare is the use of undersized CO₂ apparatus (Grandin, 2013).

Over one-third of pigs that displayed regular gasping in the present study also exhibited a positive corneal reflex, an observation that is consistent with the findings by Atkinson et al. (2012), who identified this combination as a strong indicator of insufficient stunning. The interpretation of gasping, however, remains divisive within the scientific community. Raj (1999) described it as an indicator of residual brainstem activity, whilst Holst (2001) considered it to be a potential sign of recovery. Contrastingly, Grandin (2010) argued that gasping may simply be part of the natural dying process (referred to as agonal gasping). More recently, Verhoeven et al. (2016) emphasised its welfare implications, suggesting that gasping could induce breathlessness and distress in pigs that are still conscious. This divergence in scientific opinion was also identified recently by Lindahl et al. (2025), which underscores the urgent need for both a clearer definition and standardised interpretation of regular gasping as a welfare indicator at slaughter. Establishing harmonisation is crucial not only to refine stunning assessment protocols but, more importantly, to minimise the risk of pain, stress, and suffering for animals during slaughter.

We discovered large variations in the registrations of CO2 concentration and temperature in several slaughterhouses, with values deviating from the SOPs set by the FBOs themselves. Although control system logs documented these variations, animal welfare officers (AWOs) and slaughter personnel did not consistently monitor them. Checks were typically only conducted when alarms were activated. The risk of critical parameters, such as gas concentration, falling below acceptable thresholds without any corrective action is highly concerning, as it can compromise both stun quality and animal welfare. Insufficient gas concentration has been linked to an increased incidence of symptoms indicating inadequate stunning (Rodriguez et al., 2008; Atkinson et al., 2012; Verhoeven et al., 2016). Similarly, deviations in CO₂ temperature, whether too low or too high, can alter the gas's physical properties, for example, by making it more volatile, which in turn reduces its effectiveness. We observed a lack of awareness among personnel regarding these risks and urge AWOs or designated personnel to address this issue through consistent, preferably daily, monitoring of CO₂ parameters from the logs. Monitoring and adjusting control system settings should be a prioritised response when signs of poor stun quality are observed, and this is also enforced by law (Council Regulation (EC) No 1099/2009).

4.2 Stunning efficiency for cattle

Among cattle, a total of 7.3% of animals displayed symptoms of shallow or poor stun quality, with 5.6% classified with poor stun quality, indicating a significant risk of animals not being fully unconscious after stunning, or recovering from unconsciousness before dying from blood loss. These findings are lower than reports from earlier research, where the frequency of inefficiently stunned animals was 9.2% (von Wenzlawowicz et al., 2012), 12.5% (Atkinson et al., 2013), and 31.8% for adult and young cattle of different sexes and breeds (Gouveia et al., 2009). The proportion of inadequately stunned animals in our study varied widely across the slaughterhouse visits, from 0 to 18.5%, suggesting that factors such as the type and condition of stunning equipment, as well as the skill and attentiveness of personnel (EFSA, 2020a; 2020b), play a critical role in stunning effectiveness. We also found that sex was associated with higher proportions of inadequately stunned animals with male cattle (young bulls, mature bulls, and steers) demonstrating higher rates of inadequate stunning compared to females (heifers and cows). This finding is consistent with findings from Atkinson et al. (2013), who reported that bulls were more likely to be insufficiently stunned. This underscores the need to consider animal characteristics and operator competence to enable consistent stunning outcomes.

We found a significant effect of shot accuracy on the likelihood of re-stunning, which was expected. Inaccurate shots (Figure 4) occurred in 23.4% of cattle in our study, which is substantially higher than the 8.0% reported by Atkinson et al. (2013). Notably, even among shots placed in the optimal position, 16 failed to induce an adequate stun, suggesting issues related to stunning equipment performance. In our study, most inaccurate shots were placed more rostrally, whereas previous studies reported misplacement primarily above the target area (Atkinson et al., 2013; Gregory et al., 2007). This variation emphasises the challenges of consistent shot placement (Terlouw et al., 2016) and reinforces the importance of ongoing personnel training, but also regular checks and services of the captive bolts.

An unexpected finding was that all involved slaughterhouses use guns with bolt lengths shorter than the current recommendation of 120 to 150 mm when stunning adult cattle (European Commission, 2017). Bolt length has a direct effect on brain damage (Wagner et al., 2019) and stunning efficiency; thus, this finding stresses the importance of up-to-date knowledge among slaughterhouse personnel and equipment upgrades, implying that slaughterhouse personnel require further training regarding how technical parameters of the guns affect stunning efficiency. Another important aspect is the cartridge strength, which directly influences the kinetic energy and speed of the bolt, and this must be adapted to the breed, sex, and size of the animal. Insufficient power can result in inadequate stunning, whilst excessive power can alter the performance of the bolt and increase the risk of equipment wear. Selecting an appropriate cartridge strength for the captive bolt used is therefore vital for both effective stunning and maintaining animal welfare (Gibson et al., 2015).

4.3 Sticking procedure

Of the 11 slaughterhouses included in this study (pigs and cattle), eight used knives shorter than 20 cm. Although all pig slaughterhouses used double-edged knives, only three used knives with a blade length of 20 cm or longer. Only two of the six cattle slaughterhouses used double-edged knives, and one used a knife that exceeded 20 cm. Wotton and Gregory (1986) demonstrated that the use of a 20 cm double-edged knife significantly reduced the likelihood of poor sticking and bleeding in pigs. Improper sticking, i.e., when the sticking wound is too small or inaccurately placed, can result in slow exsanguination and increase the risk of animals regaining consciousness (Anil et al., 2000; Brandt and Aaslyng, 2015). Studies have shown that brain responsiveness, and hence loss of consciousness, can persist for 14 to 23 s in pigs that are slaughtered without previous stunning (EFSA, 2004; Wotton and Gregory, 1986) and between 19 to 323 s in cattle bled without prior stunning (Newhook and Blackmore, 1982). For large-sized animals, or if the cut is incomplete, this time may be longer. In our observational study, we did not explicitly assess the association between knife length, blood loss, and stunning efficiency, but this is another factor that may warrant further attention.

This observational study had certain limitations in its design, as it did not consider the training or experience of the operators in the assessment of stun quality. First, due to confidentiality, detailed slaughterhouse-specific data could not be disclosed. Second, because this was an observational study, certain technical parameters (e.g., CO₂ settings) could not be evaluated for each cage of pigs. Future studies should therefore aim to include these registrations for each animal. Additionally, the presence of the observer may have positively influenced the slaughterhouse personnel's behaviour; for instance, they may have been more vigilant in recognising signs of insufficient stunning or more inclined to re-stun when uncertain in the presence of an external observer. Lastly, ethical concerns arose when the observer could not intervene in cases of stun failures not detected by slaughterhouse personnel.

This study enriches the existing scientific literature by providing key insights into how the time between stunning and sticking affects stun quality and the risk of exposing animals to unnecessary suffering at slaughter. Inadequate stunning not only compromises animal welfare (Cockram, 2020) but also disrupts operational efficiency (Grandin, 2000), with potentially increased costs due to process delays, additional labour (Jerlström et al., 2022), restunning, and greater resource use (e.g., ammunition). These findings underscore the importance of managerial factors influencing stun quality, such as equipment maintenance, training of personnel, and adherence to standard operating procedures. It also stresses the importance of adapting improvements to each slaughterhouse situation and circumstances. The variation in stunning efficiency across slaughterhouses necessitates regular support from equipment manufacturers, auditors, and regulatory authorities.

Further research is needed to validate gasping as a welfare indicator at slaughter, distinguishing it from rhythmic breathing, preferably by using EEG to assess brain activity (Forslid, 1987; Hjelmstedt et al., 2022). Future studies should also explore the physiological and neurological relevance of gasping across different gas concentrations and gas exposure durations. Additional studies on the effectiveness of training programmes for slaughterhouse personnel, especially regarding symptoms of inadequate stunning, appropriate re-stunning procedures, and monitoring of equipment, are also needed. Another priority is research on the development of real-time monitoring technologies, such as motion sensors or AI-based vision tools, which could enable a continuous, objective detection of signs of failed stunning, post-stunning recovery, and equipment failure during stunning.

4.4 Conclusions

The findings of this study show that longer stun-to-stick intervals are associated with an increased risk of inadequate stunning, i.e., with deviations in stun quality, in both pigs and cattle. Longer intervals are also associated with a higher likelihood of re-stunning. Stick times of less than 59 s for pigs and 99 s for cattle were associated with the lowest rates of inadequate stunning. Consequently, any extension of the stun-to-stick interval requires thorough, case-by-case evaluations based on the specific conditions of each slaughterhouse. Notably, the slaughter personnel failed to detect 10 pigs and 13 cattle that exhibited signs of inadequate stunning. These animals proceeded through the slaughter line, possibly still conscious, without proper monitoring or re-stunning. This raises concerns regarding the detection of deviations in stun quality, directly impacting animal welfare at slaughter, as these animals may have experienced unnecessary suffering. Furthermore, the variation in stun quality between slaughterhouses suggests the potential for improving stunning practices in slaughterhouses with high rates of stunning failures. The results of this study emphasise the need for further research and development related to optimal stun-tostick intervals adjusted to the specific conditions of each slaughterhouse, establishing and implementing robust SOPs for stunning, monitoring, and maintenance of stunning equipment (e.g., CO₂ parameters and bolt lengths), along with recurrent training for slaughter personnel.

Data availability statement

The datasets presented in this article are not readily available due to GDPR and non-disclosure agreements between the slaughterhouses and SLU. All data required to replicate this work are provided (in aggregated form) in the article tables and figures. Requests to access the datasets should be directed to josefine.jerlstrom@slu.se.

Ethics statement

The animal study was approved by Swedish Animal Research Ethics Committee in Gothenburg. The study was conducted in accordance with the local legislation and institutional requirements. (Ethical approval number: Idnr 005587; Dnr 5.8.18-07913/2023).

Author contributions

JJ: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. CB: Conceptualization, Funding acquisition, Supervision, Writing – review & editing. AW: Conceptualization, Data curation, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fanim.2025.1633616/full#supplementary-material

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