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The slaughter of animals comprises the induction of unconsciousness followed by bleeding to cause death. Today’s slaughter practices are chosen to avoid animal suffering, but what does science tell us about animal suffering? Do animals have emotions? Consciousness? How to study consciousness? Experiments suggest strongly that animals have emotions and are conscious, although many aspects of consciousness are still not understood. However, various brain areas involved in consciousness have been identified and the mechanical, electrical and gaseous stunning techniques used at slaughter, cause dysfunction of one or several of these areas, in different manners to induce unconsciousness.

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Introduction

This article discusses first, current knowledge on animal emotions and consciousness and second, how this knowledge relates to slaughter techniques. 'Animals' refers to non-human mammals. Mostly, slaughter involves two interventions: first, the animal is stunned to induce unconsciousness and second, the animal is exsanguinated to induce death. Manipulation of the animal, such as hoisting and bleeding, is allowed if indicators ensure the durable unconsciousness of the animal. Further processing of the animal, such as removal of legs, head, or hide, is only allowed in the absence of signs of life.

The reason for the induction of unconsciousness before bleeding is the assumption, for some, or the conviction, for others, that animals can suffer and the belief that humans have the moral obligation to avoid suffering of the animals they are responsible for [57]. Can animals suffer? To answer this, we need to ask whether animals have emotions, and whether they are conscious of them [2,11,43,32].

Emotions in humans and animals

'Emotion' can be described as the mental state that accompanies specific appraisals, related to the bodily state, such as being hungry or replenished, or to the environment, for instance, the presence of an apparent threat, a potential mate or tasty food. Examples of emotions are fear, aggression, frustration, affection or unfulfilled desires [3,28,48]. They are difficult to study due to their subjective component, and for many years, farm animal scientists preferred to study farm animals when the latter had 'difficulties adapting' to environmental or physical constraints [18]. This state was referred to as 'stress' and the 'difficulties to adapt' referred to physiological and behavioural responses to challenges: these we could measure and were further related to their productive capacities.

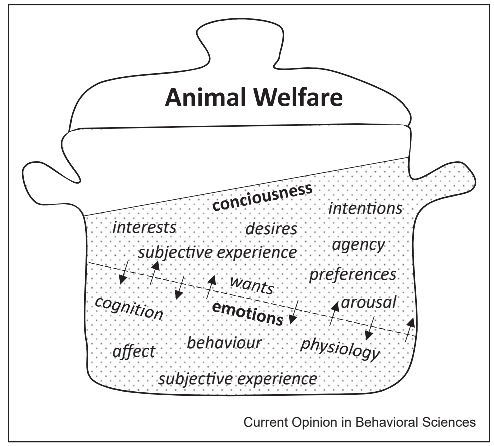
Although little studied, the subjective emotional state associated with stress in farm animals and humans was acknowledged throughout the twentieth century [5,25,40,10,4,15] and later [58,12,64]. Subsequently, new concepts and paradigms were used to study of emotions of farm animals [28,3,43,66]. These paradigms were partly inspired by studies on emotions in humans, initially using verbal self-reporting, but subsequently using facial, behavioural and physiological responses. They demonstrated that the emotion elicited by a situation depends on several well-defined characteristics of the situation [52]. For example, a situation with a high degree of suddenness, and low familiarity, predictability, controllability and pleasantness, evoked negative emotions, such as fear and anger [36]. Adopting these techniques found that animals are also capable of recognising these characteristics. For instance, when a piece of textile fell rapidly and unexpectedly behind the trough from which sheep were eating, they showed startle responses and a short-lasting rise in heart rate, indicative of a change in emotional state. The sheep did not react when the object fell slowly and reacted less strongly when a light signal announced the appearance of the textile [65]. Overall, the results showed that sheep are sensitive to suddenness, predictability and familiarity and that they can form expectations [22]. It was suggested that most or possibly all mammals are sensitive to the suddenness, unfamiliarity and predictability of their environment, and are capable of a range of emotions, such as fear, anger, rage, despair, boredom, disgust and happiness [65]. Hence, stress in animals can be described as a negative emotional state, associated with behaviour and physiological responses aiming to protect the animal against a perceived threat, whether real or imaginary [65,60]. Animals experience also positive emotions [65,17]. For instance, stroking can be used to reward farm animals and to facilitate subsequent handling [49]. Both negative and positive emotions help the animal to adapt, because emotions are important drivers of motivation [60].

The neurological systems controlling emotions and related functions in humans and non-human mammals show many similarities. The limbic system, involved in emotional reactions in humans, is also present in non-human mammalian brains and consists of essentially the same structures [34]. Their functioning is also similar. For example, the amygdala, which is part of the limbic system, is involved in fear. Blocking its functioning stopped the immobility response of rats to fear-inducing stimuli, such as cat odour [8]. In Rhesus monkeys, blocking the amygdala reduced fear responses to snakes [16]. Humans with amygdala damage do not exhibit physiological defence responses to threat [33]. However, emotional processes are complex and so are the underlying neurological substrates. Although given structures of the limbic system may have specific functions, the processing of emotions is best described as the output of the integrative functioning of the limbic and other networks, including the cortex [67].

Emotions and consciousness

As mentioned, it is believed that for an animal to be able to suffer, not the mere presence of emotions, but emotions the animal is conscious of, are needed. Already in 2012, the Cambridge Declaration on Consciousness declared that '*Convergent evidence indicates that non-human animals have the neuroanatomical, neurochemical, and neurophysiological substrates of conscious states along with the capacity to exhibit intentional behaviors*', and that '*humans are not unique in possessing the neurological substrates that generate consciousness. Nonhuman animals, including all mammals and birds, and many other creatures, including octopuses, also possess these neurological substrates.*' New concepts and experimental paradigms and modern, sophisticated brain imagery techniques continue to improve the scientific understanding of human and animal consciousness [29,35,45]. Following Birch [2], today the question is not *if*, but *how* animals are conscious. Despite this progress, as for emotions, there is not a single, consensual definition for consciousness. A good working definition is 'a state of mind in which there is knowledge of one's own existence and of the existence of surroundings' [9]. This 'knowledge' refers to the construction of an integrated mental image from the information perceived from the environment and the body, and the information obtained through memories and other sources [29,9,42]. The construction of such an image needs a range of processes involved in the acquisition, storage and manipulation of information. Emotions are part of the building blocks constructing this integrated image ([32,41,48]; Figure 1). This image, containing the 'self', with needs and desires, in a surrounding world that may offer opportunities to fulfil these needs and desires, is accessible, that is, inside the realm of usable knowledge, and foundational in making choices and decisions. Another important aspect of consciousness is the subjective experience, that is, the way things feel. This part is difficult to study, called 'the hard problem' of consciousness [6].

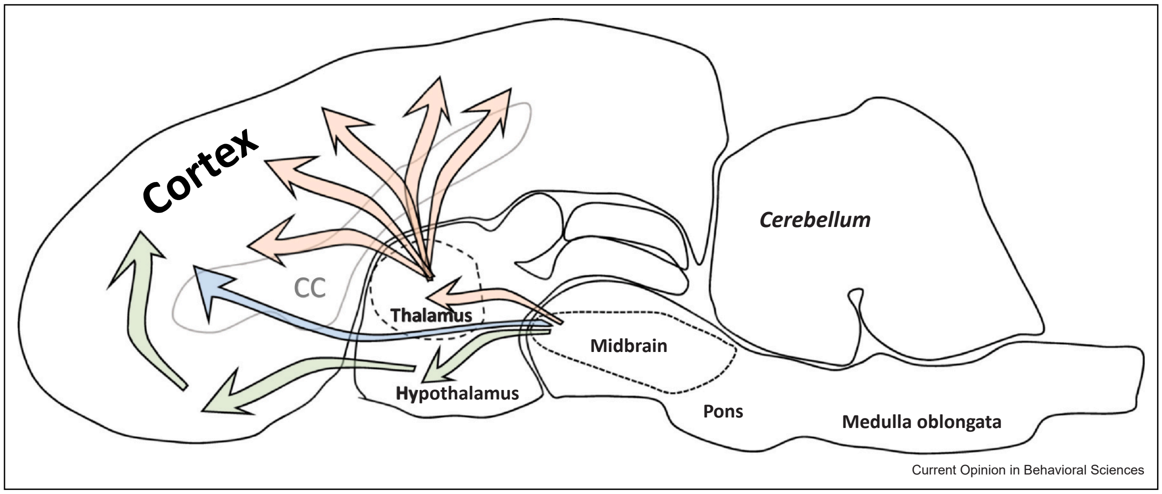
Figure 1



Animal welfare is considered to be related to the capacity of the animal to have emotions and to be conscious of them [43]. No uniform consensual definitions or descriptions exist yet for emotions or consciousness, but different components or aspects have been described [28,32], shown in the brewing pot. Their exact roles and ways of interactions remain to be understood.

The construction of such complex mental states involves many brain areas. The visual, auditory, somatosensory, gustatory and olfactory cortices are primary cortices: they receive information from the senses and carry out the first decryption of sensory signals. The frontal, temporal, parietal, cingulate and insular cortices are the association

Figure 2



Schematic reproduction of a sheep brain (midsagittal cut). Studies on humans and animals show that the cortex is involved in the *content* of consciousness, and the ascending reticular-activating system, with nuclei in the midbain and pons, in the *level* of consciousness. The ascending reticular- activating system comprises three main pathways: via the thalamus located just above the brainstem (orange arrows), via the basal telencephalon (green arrows) and directly (blue arrow). The thalamus is further involved in the integration of sensory and other types of information.

cortices: they are essential for the interpretation and the integration of the information into a larger image and for planning the appropriate responses [1,9]. Specific neurological networks control the various related higher-order functions [27]. For example, in humans, executive task performance depends on a network contained in the frontal and parietal cortices [55]. Emotion-linked decision-making is supported by a network in the temporal and orbitofrontal cortices [27,30]. Certain subcortical areas, such as the thalamus, essential for the integration of sensory and other types of information, contribute to these higher-order functions.

Consciousness has two major components: content and level [20]. Cortical activity relates to the content of consciousness. The level of consciousness refers to the level of arousal, and depends on activity of the reticular formation in the brainstem (Figure 2). This structure stimulates the cortex: its lesions or ascending projections cause a comatose state [9]. The structures essential for consciousness in humans, primary and association cortices, and subcortical areas, such as the thalamus and limbic system, and the reticular formation in the brainstem, are also present in animal brains [32]. Their functional connections have similarities, but also some differences. For instance, the orbitofrontal cortex has key functions in the representation of emotions and of rewards and non-rewards in humans [50]. Monkeys and humans have essentially the same orbitofrontal cortical areas with a similar connectivity [50]. However, although the rodent reward system does include the orbitofrontal cortex, it has a very different connectivity and some of the areas observed in humans and other primates do not exist [50]. Data on farm animal brains are less detailed, but anatomical studies show that they are similar to those of other mammals [51]. Close similarities exist also between pig and primate brains with respect to anatomy, growth and development, with similar neuroarchitectures in the striatum and subthalamic regions, and similar cortical convolutions, shape and total number of neocortical neurons [37,53]. Overall, the analogies suggest that like all mammals, farm animals are conscious and have conscious emotions, with many similarities but also differences compared with humans, from the neurological, behavioural and physiological perspective.

Although various brain processes involved in the emergence of consciousness have been described, shared reflections between physicist and scientists with medical training have led to suggestions that more subtle processes may also play a role [19,24,54]. Electromagnetic fields, photons and quantum processes were suggested to contribute to the emergence of consciousness [19,24,54]. There are certainly characteristics of consciousness that remain difficult to understand using classical neurobiological knowledge. For example, scientific studies of near-death experiences suggest that 10–20% of cardiac arrest survivors may report detailed descriptions of the resuscitation, corroborated by resuscitation staff, despite that brain function ceases during cardiac arrest [63,46,23,38]. Survivors that claim to have no memory are unable to describe the events accurately [23]. The large majority of the former group of survivors report further the absence of pain and distress [7,31,38]. Such reflections underline that further research, possibly combining different disciplines, is still needed to understand consciousness, not only in humans, but also animals [2,38,47].

Consciousness is also debated in the philosophical realms. Subjective mental states are strictly personal: how can we prove that humans other than ourselves, let alone animals, are conscious? Would our societies function the way they do if humans were simply robots, without any subjective experience [6,13,14,26]? Animal scientists agree on the difficulty to prove formally the presence of subjective experience in animals, but indicate that, pending further knowledge, for the sake of precaution, we should assume that animals consciously perceive their inner mental state, including emotions [48].

Consciousness and slaughter

Whether consciousness is derived from, or transmitted through brain activity, will not change the basic principles of slaughter techniques. There is little research on the relationships between consciousness and brain functioning in farm animals; hence, our knowledge is based on studies in other species (Figure 2). We assume that farm animals, such as other animal species, are able of consciously experiencing negative emotions and that the unconscious state ensures that the animal does not experience pain or fear during the bleeding process. Below, we describe the different slaughter techniques, and the evaluation methods to assess the state of consciousness/unconsciousness of the animal. Stunning techniques are mechanical, electrical or use gas. The technique used depends on the species, essentially for practical reasons [61]. Following stunning, exsanguination must take place sufficiently rapidly to ensure that the animal does not regain consciousness during the bleeding process. This obligation has specific relevance when reversible stunning techniques are used.

Penetrating captive bolt stunning uses a stun gun fitted with a captive bolt (cattle, sheep and sometimes pigs)
Fired when placed on the head of the animal, the bolt enters the brain before retracting back into the gun [61]. Loss of consciousness is caused by several phenomena (Table 1). When hitting the skull, a shock wave spreads through the brain structures, causing tears and lesions of the brain tissues, disturbances of blood flow and depolarisation of neurons in the cerebral hemispheres and often the brainstem. As a result, the functioning of neurons is disturbed, preventing the brain from correctly integrating information from the body and the environment. Depending on the intensity and location of the impact, consciousness is reduced or even suppressed. This effect is most often temporary.

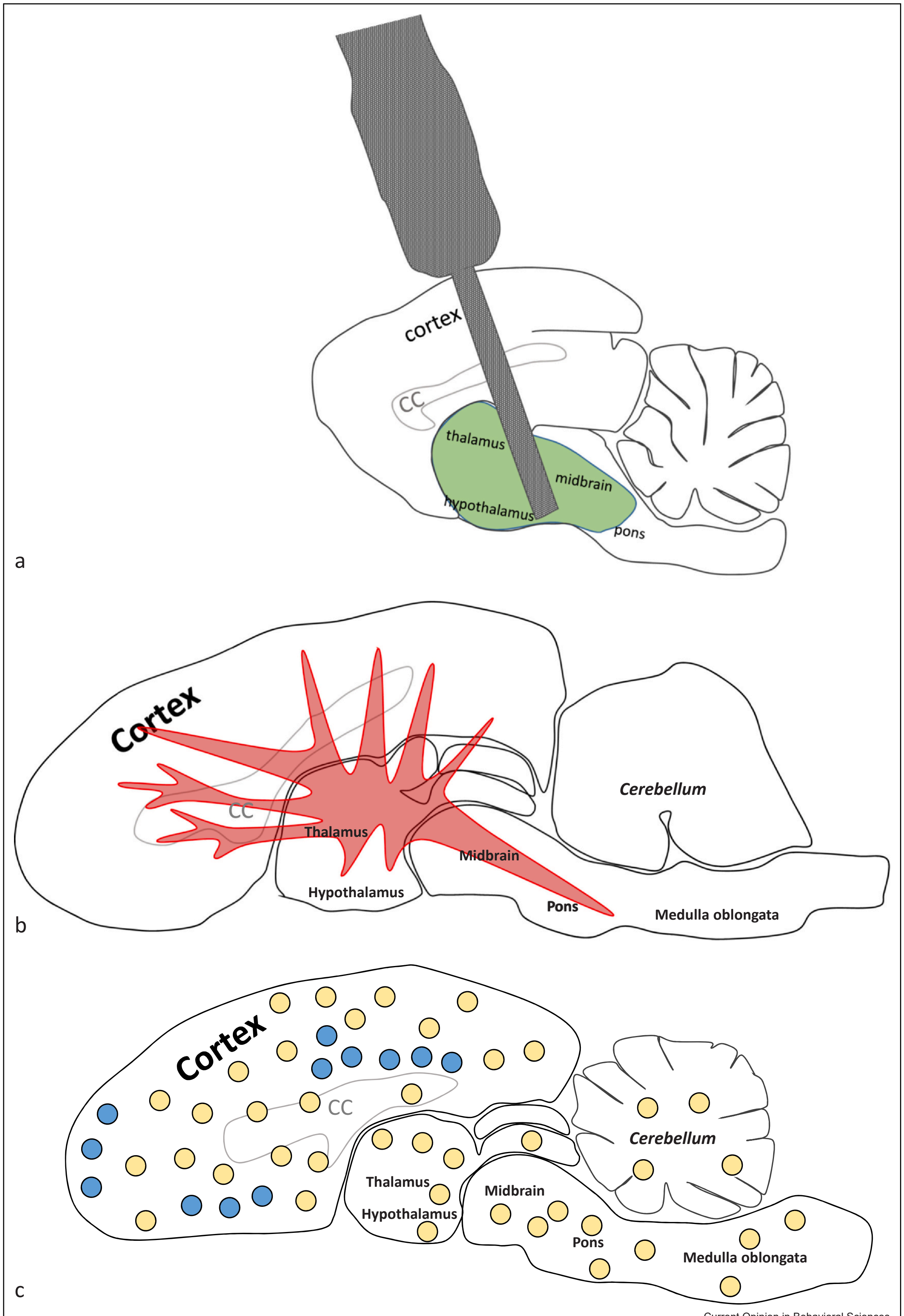
The entering of the bolt in the brain destroys tissues in and surrounding its path. Brain tissue sucked into the empty space created during its withdrawal causes additional damage. The bolt targets the thalamus and/or the ascending reticular-activating system, to interrupt the activation of the cortex, thus inducing permanent unconsciousness (Figure 3a). Accompanying haemorrhages lead to increased intracranial pressure and deprive cerebral structures of blood supply, preventing them from functioning (Table 1). The latter two effects are

Table 1

Different stunning techniques, and bleeding without stunning: physiological consequences and reversibility of the effects.

Effects	Physiological consequences	Reversibility
Penetrating captive bolt stunning		
Shock wave	Excessive influx and efflux of ions: depolarisation of nerve cells Slowing of energy production by cells Tissue compression: decreased neuronal functioning	Potentially reversible
Passage of the bolt through the brain	Tissue compression: decreased neuronal functioning Tears and ruptures of brain tissue Vessel tears	Potentially reversible Irreversible
Brain hemorrhage	Insufficient blood circulation: lack of glucose and oxygen leading to a lack of energy in the brain cells Tissue compression: decreased neuronal functioning	Irreversible
Electrical stunning		
Current through the brain	Synchronised depolarisation of nerve cells, spreading to other areas of the brain	Reversible
Current through the heart (head–body technique only)	Cardiac fibrillation: slow blood flow Weakness of skeletal muscle (–> reduction in clonic contractions)	Potentially reversible Reversible
CO_2 stunning		
Absorption and dissolution of CO_2 in the blood	Acidification of brain cells	Reversible or irreversible depending on exposure time and CO2 concentration
Bleeding without stunning		
Massive bodily hemorrhage causing reduced cerebral blood flow	Lack of glucose and oxygen leading to lack of energy in brain cells	Irreversible

Figure 3



Current Opinion in Behavioral Sciences

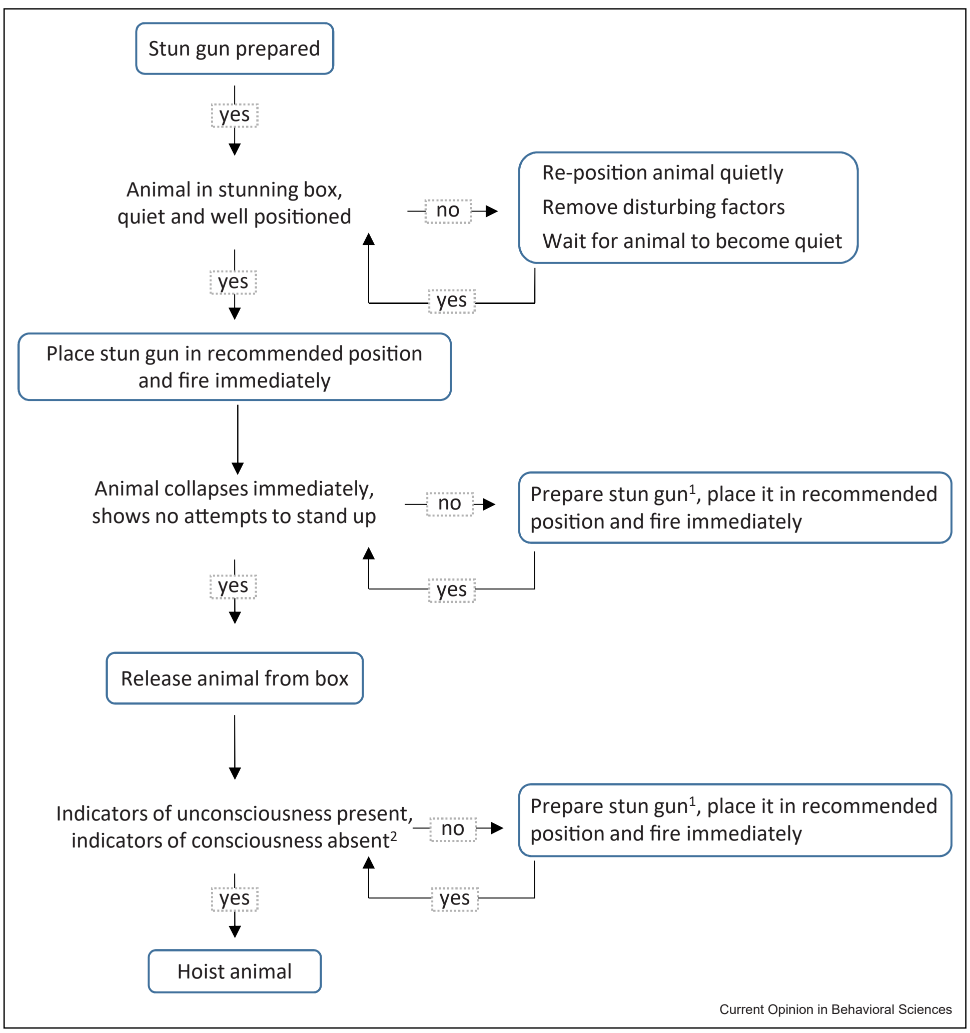
Illustrations of the functioning of the different stunning techniques. **(a)** Median cut of a bovine brain. Penetrative captive bolt stunning: the penetrating bolt aims to lesion parts of the thalamus, hypothalamus, mesencephalon and/or pons. CC=corpus callosum. **(b)** Median cut of a sheep brain. The electrical current spreads via the thalamus to other brain regions, causing an epileptic-like fit resulting in temporary unconsciousness. **(c)** Median cut of a pig brain. Inhalation of high concentrations of CO2 causes acidification of the blood and consequently of brain cells. This causes slowing of brain activity across the brain (illustrated by yellow circles, [68]). Functional connectivity MRI found significant reduction in the size of the cluster volume of the posterior cingulate cortex, bilateral inferior parietal cortex, medial frontal cortex and bilateral medial temporal lobe of the cortex (illustrated by blue circles, [68]), which all play a role in the content on consciousness. MRI; Magnetic Resonance Imaging.

irreversible. Mechanical stunning induces instantaneous loss of consciousness.

Electrical stunning (poultry, pigs and calves)

During 'head-only' electrical stunning, an electrical current passes through the brain via head electrodes, and triggers an epileptic seizure involving the thalamus, brainstem and cortex (Table 1; [61]; Figure 3b). The seizure is followed by a period of greatly reduced brain activity due to the massive, synchronised depolarisation. During the seizure and as long as the neurons are depolarised, the animal is unconscious. In addition, the current causes a tonic phase, characterised by contracted muscles, followed by clonic phases characterised by convulsions. Gradually, the neurons recover and the animal regains consciousness [61]. The effect is

Figure 4



Example of a flow diagram for penetrative bolt stunning to help decision-making. [1.] Following an incorrect stun, the operator inspects the correct functioning of the stun gun and may decide to change the gun, or the ammunition used, for example. [2.] Slaughterhouses have their own standard operating procedures that indicate which indicators should be used.

therefore reversible. The 'head–body' method includes, in addition to the two electrodes on the head, a third electrode in the heart region to cause cardiac fibrillation. The resulting reduction of blood flow aggravates cerebral hypoxia, prolonging the state of unconsciousness induced by the head electrodes. Only if cardiac arrest occurs, the method is irreversible [59,61]. Electrical stunning induces unconsciousness instantaneously.

Gas stunning (pigs, poultry)

The animals are immerged in a gas mixture containing high CO_2 concentrations. The CO_2 is absorbed into the blood, acidifying it, which in turn acidifies brain cells ([39,56]; Table 1). Their metabolic rate slows as a result, leading to unconsciousness ([61,68]; Figure 3c). The loss of consciousness during gas stunning is gradual. During the induction, animals often show reactions indicative of aversion to the method.

The stunning techniques must be applied correctly, using properly maintained equipment, and the state of consciousness of the animal must be evaluated, using indicators of consciousness, of the risk of consciousness and of unconsciousness [59]. Only indicators of unconsciousness are presented here: their presence allows hoisting and bleeding of the animal (Figure 4). Mechanical and gas stunning use the same indicators occurring immediately and progressively, following mechanical and gas stunning, respectively. The persistent loss of standing posture, without righting attempts, indicates that the red nucleus and/or its caudal projections no longer function. The absence of a corneal reflex indicates that the caudal part of the pons and/or rostral part of the medulla oblongata do not function. The absence of breathing indicates that the caudal part of the medulla oblongata does not function. The simultaneous absence of these three functions indicates that the regions containing and/or caudal to the ascending reticular-activating system, do not function, ensuring that consciousness will not return before the end of bleeding. Immediately following electrical stunning, the absence of the standing posture and the presence of a 10-s-lasting tonic phase are used as indicators of unconsciousness; the corneal reflex and breathing cannot be used during the early post-stun period, due to the interferences of the tonic and clonic reactions. If the indicators do not ensure a durable unconscious state, the animal is immediately stunned again by a back-up stunning technique.

Direct bleeding without prior stunning of the animal may be used during religious slaughter. The haemorrhage-induced lack of oxygen and glucose in the brain leads to a progressive decrease in the level of consciousness caused by a slowing of brain activity. Progressively, the nerve cells of the brain, including those responsible for vital functions (respiration, homoeostasis and regulation of body temperature), are irreversibly damaged and the animal dies. The indicators of unconsciousness, absence of the standing posture without righting attempts, absence of the corneal reflex and respiratory arrest, appear progressively during the bleeding process [62].

Concluding comment

Application of relatively rudimentary stunning procedures has started at the beginning of the 20th century. Although the need to immobilise the animal was an important aspect, the need for 'humane' slaughter conditions was put forward from the beginning [21,44]. Present-day neurological knowledge indicates that stunning stops higher-order brain functioning: the animal has no longer knowledge of its surroundings, and its bodily and emotional state, thus avoiding needless suffering. In addition to classical neurobiological mechanisms, other, more subtle processes possibly contribute to the emergence of consciousness but this needs further research.

Data Availability

The authors are unable or have chosen not to specify which data have been used.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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