

## Stress at slaughter in cattle: role of reactivity profile and environmental factors

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### Abstract

During slaughter, cattle may be exposed to many potentially stress-inducing factors, of emotional and physical nature. A series of studies aimed to identify factors that may contribute to slaughter stress. During reactivity tests testing emotional stressors, Blond d'Aquitaine bulls were more reactive than Angus and Limousin bulls. However, no breed differences were found for stress indicators at slaughter. Indicators of post mortem (PM) muscle metabolism were correlated with stress reactions at slaughter, and with behavioural reactions and heart rates during the reactivity tests, including a sudden event and handling. Similarly, in Normand cull cows, stronger behavioural and physiological reactions during the slaughter procedure were associated with faster PM muscle metabolism. Reactions during the reactivity tests were also correlated with stress indicators at slaughter. A Principal Component Analysis indicated that the first and second axes were correlated with reactions to non-familiarity and to social isolation, respectively. Both axes were correlated with stress indicators at slaughter, suggesting that these two aspects contribute significantly to the emotional stress at slaughter. These experiments indicate that stress reactivity at slaughter may be predicted from behavioural and emotional stress reactions during reactivity tests. A third experiment found that compared with normally fed cows, 30-h food-deprived cows showed stronger startle and fear responses in response to a sudden event. Within a group subjected to a physical-effort treatment, compared to normally fed heifers, food-deprived heifers were more reactive to human exposure. This shows that the reactions to a given stressor may increase due to the presence of other stressors. Thus, in cattle, novelty, social disturbances and sudden events may contribute to slaughter stress and the simultaneous presence of several stressors during the slaughter period may exacerbate stress reactions.

**Keywords:** animal welfare, cattle, emotional stress, meat quality, physiology, slaughter

### Introduction

#### Ethical questions

Throughout the pre-slaughter period, animals may show stress reactions. Stress has often been described in terms of the capacity of the animal to adapt, behaviourally and physiologically, to environmental challenges (Fraser *et al* 1975; Broom 1987). Accordingly, in the slaughter context, the effects of transport duration and food deprivation have been much studied (Warriss *et al* 1984; Cockram *et al* 1997; Knowles *et al* 1999). While it is important to understand the impact of physical challenges on the physiological and behavioural adaptive capacity of the animal, scientists have repeatedly reminded that animals are capable of emotional experiences (Dawkins 1980; Duncan 1996; Dantzer 2002; Désiré *et al* 2002). (NB In this paper by 'emotional experiences' and 'emotions' we mean subjectively experienced feelings). For example, many behavioural reactions and patterns in non-human mammals are related to brain systems known to be involved in emotions in humans (Panksepp *et al* 2002; Damasio 2003). Therefore, there is little reason to doubt that in non-human mammals, stress

has a psychological or emotional dimension as it does in humans (Mason 1974; Terlouw 2005). We may consider that a farm animal is stressed if it experiences negative emotions (Veissier & Boissy 2007). There are two consequences to the acceptance that animal stress has an emotional dimension. First, stress in farm animals should be avoided as much as possible for ethical reasons. Without the emotional dimension, animals could be considered as objects, for example, cars; if a sports car has difficulties to adapt to a sand track, there is no welfare or ethical problem for the car. Second, the stress status of an animal is subjective: it depends on the way the animal evaluates its environment. These two points suggest that we need to avoid stress at slaughter as much as possible, by taking into account the animal's evaluation of its environment.

#### Possible causes of stress at slaughter

To reduce animal stress at slaughter, we need to understand its causes. The pre-slaughter period is a complex period with various stages (Terlouw *et al* 2008). Before leaving for the abattoir, animals may be gathered on a loading platform or in a pen to facilitate subsequent loading. Pigs, but also

animals of other species, may have had food withheld to avoid travel sickness, or for convenience or financial reasons. The animals are subsequently loaded, transported and unloaded at the abattoir. Loading, unloading and transport conditions depend on the facilities on the farm and at the abattoir, and on the layout of the truck, the driving style and distance travelled. After unloading, animals are either directly slaughtered, or may wait for several hours, often overnight, in the lairage area in the abattoir.

The above describes the slaughter procedures from the human point of view. As indicated above, we need to understand how the animals evaluate these different slaughter stages in terms of stress, or negative emotions. The stressors encountered during the slaughter period may be distinguished in different categories. Some forms of stress have a physical origin, such as food deprivation, fatigue or pain, although these forms of stress have probably also an emotional component (Horswill *et al* 1990; Danziger 2006). Other forms of stress have an emotional origin, such as unfamiliarity, human presence and disturbance of the social group. For example, unfamiliarity may cause fear that negative or aversive experiences may lie ahead (Boissy 1995). Some aspects of the slaughter period may be associated with both physical and emotional stress. For example, inter-animal aggression may result in both fear and pain (Terlouw *et al* 2008). Abattoirs may have inappropriate lighting and many of them are very noisy (Grandin 2006) and very loud noises or bright light may be physically uncomfortable. Sudden events may also be a cause of stress (Grandin 1999) and may cause immediate responses in the animal, such as startle (Greiveldinger *et al* 2007), even before the animal has been able to identify the exact nature of the stressful stimulus (Jordan & Leaton 1982).

Thus, during the slaughter procedures, animals are subjected to many potential stressors, simultaneously and successively, in a series of different environmental contexts. This complex situation makes it difficult to identify which aspects of the environment animals react to. In addition, reactions to a given stressor may be modified by the presence of other stressors. For example, in heifers, the presence of a fearful conspecific increases the startle response to a sudden event (Boissy & Bouissou 1995). To understand the way animals evaluate the slaughter situation, we have chosen to study, in the first instance, reactions of animals to simplified situations where they are presented with stimuli that may cause emotional stress. It is important, however, to take into account that animals have probably an integrated view of their environment. Therefore, subsequently, we have studied whether the reactions of cattle to a given emotional stressor may be changed by the presence of other, additional stressors, such as food deprivation or physical effort.

### Stress and meat quality

Improving slaughter conditions for animals is not only important for ethical reasons, it may also have consequences for meat quality. Meat quality is influenced by post mortem muscle metabolism which, in turn, may be

influenced by pre-slaughter stress reactions (Bendall 1973). After bleeding, muscle energy metabolism is modified: nutrients and oxygen are no longer supplied to the muscle and metabolites accumulate. The dephosphorylation of ATP and anaerobic glycogenolysis result in the accumulation of protons and lactate and, thus, in acidification of the muscle (Bendall 1973). Exercise and psychological stress just before slaughter increase muscle metabolic activity, which may continue after death, resulting in faster post mortem decline in pH (low early post mortem pH) and slower muscle temperature decline (Bendall 1973; D'Souza *et al* 1998; Rosenvold & Andersen 2003). Increased stress and/or activity during the pre-slaughter period may cause further depletion of glycogen stores, resulting in a lower overall pH decline (high ultimate pH; Bendall 1973; Terlouw & Rybarczyk 2008). It is well documented in all species that high levels of stress during the slaughter period may result in meat with relatively high ultimate pH as reviewed by Terlouw and others (2008). The effects of stress on the early post mortem pH decline are more specifically documented for poultry and pigs: there is little information for cattle (for a review, see Terlouw *et al* 2008). As post mortem muscle metabolism may be an indicator of pre-slaughter stress and have consequences for subsequent meat quality, it may be relevant to measure variables related to muscle metabolism following experimental slaughter.

## Scientific approach

### Experimental paradigms

We designed a series of experimental paradigms with the objective of identifying which aspects of the slaughter procedures may be most stressful to cattle. In all experiments, animals were subjected to controlled situations containing only a few emotional stressors similar to those that may be encountered at slaughter, and reactions were measured. In Experiments 1 and 2, these reactions were compared with stress reactions during experimental slaughter. In Experiment 1, 72 young bulls of three breeds, Angus, Blond d'Aquitaine and Limousin were subjected to a human exposure test and a surprise test (see below) before being experimentally slaughtered (5-min transport followed by slaughter at the experimental abattoir of the institute, no electrical stimulation of the carcass) at 18 months of age. In Experiment 2, 16 Normand cull cows were subjected to a social isolation and human exposure test (see below) before being experimentally slaughtered (15-min transport, 30-min forced walk through an unfamiliar labyrinth, 15-min transport, slaughter in the experimental abattoir of the institute; no electrical stimulation). In Experiment 3, the effect of additional stressors applied immediately before the reactivity test on stress reactions in reactivity tests was determined to understand how several stressors may interact (Table 1). In Experiment 3, 32 Holstein heifers and 16 Holstein cull cows were used. During the reactivity tests, half of the heifers and half of the cows had been food deprived for 30 h, the others were normally fed (controls). Within each group of the normally fed and food-deprived heifers, half of the animals were subjected to an additional

effort treatment before the reactivity test, consisting of a 5-min forced walk over 240 m in a labyrinth. Before the food-deprivation treatment, all animals had been subjected to the reactivity tests to verify that the different treatment groups did not differ before the treatments were applied. Animals used in Experiments 1 and 2 had been purchased from different commercial farms four months prior to the start of the experiments. They were kept from purchase to slaughter in an experimental barn of the institute in 6 × 6 m (length × width), straw-bedded pens in stable groups of four animals to a pen. They were fed twice daily by a familiar stockperson. Animals used for Experiment 3 were already owned by the experimental farm. They were kept in the same barn and in the same conditions as those of the Experiments 1 and 2, apart from the absence of feeding during the food-deprivation periods.

Behavioural and physiological measurements (heart rate, plasma cortisol) were used to assess stress reactions during stress reactivity tests. During experimental slaughter, the same measurements were used, as well as urinary cortisol and catecholamine levels. After slaughter, 40 min, 3 h and 30 h post mortem, muscle temperature and pH were measured as indicators of post mortem muscle metabolism.

### Reactivity tests

#### *Human exposure (and social challenge — Experiments 1, 2 and 3)*

The test was conducted in a 6 × 6 m (length × width) test arena (concrete floor and 2-m high solid walls). In the first phase, the tested animal remained alone in the test arena during 30 s (Experiments 2 and 3) or 45 s (Experiment 1). Subsequently, a familiar stockperson in unfamiliar clothing (a scarf, a hat and a red coat were added to the usual clothing) equipped with a stick (1 m) entered the test arena and remained stationary in the centre of the test arena (phase of stationary human). Thirty (Experiments 2 and 3) or 45 s (Experiment 1) later, the stockperson moved the animal into a previously identified handling zone of the arena (phase of moving), where he tried to keep the animal for 30 s (phase of detainment). If this succeeded, the stockperson carried out a series of strokes (phase of stroking). In Experiment 1, for security reasons, only five strokes were given on the thigh after which the test was stopped. In Experiment 2, animals had a view of their pen-mates and the handling zone was situated at the pen side opposite to where the pen-mates were (ie handling involved social challenge). In Experiments 1 and 3, animals were tested in social isolation throughout. In Experiments 1 and 3 the test environment was unfamiliar, while in Experiment 2, it was familiar. In Experiment 2, 5 strokes were given successively, firstly at the level of the top of the thigh, then the back, the neck and finally the cheek.

#### *Surprise test (opening umbrella) in an unfamiliar environment — Experiment 1*

The test was conducted the day after the human exposure test in an unfamiliar 12 × 0.8 m (length × width) straight corridor (concrete floor and 2-m high solid walls). During the first phase, the umbrella was absent and the tested bull

**Table 1** Experimental lay-out of Experimental 3.

Treatment	No additional effort treatment	Additional effort treatment
Fed normally	8 heifers, 8 cull cows	8 heifers
30-h food deprived	8 heifers, 8 cull cows	8 heifers

was maintained in the umbrella zone of the corridor via an iron bar placed across the corridor behind the animal at 1-m height and 3 m from the site where the umbrella would be presented (phase 1: absence of the umbrella). Thirty seconds later, an experimenter introduced the umbrella (red coloured, 50 cm) in front of the bull (at 20 cm pointed towards his muzzle) via an aperture located in the exit door (phase 2: closed umbrella). During this phase (30 s), the animal was maintained in the umbrella zone of the corridor and could interact freely with the closed umbrella. Subsequently, the umbrella was opened while, at the same time, the horizontal bar was removed by a second experimenter allowing the animal to walk freely forwards and backwards through the corridor (phase 3: opened umbrella). During this phase (30 s), the bulls could interact with the opened umbrella. If the head of the animal was turned at the end of phase 2, the experimenter waited for the animal to orient its head towards the umbrella before opening it to standardise the distance between the muzzle of the animal and the umbrella at the time of opening.

#### *Surprise test (air blast) in a feeding context in an unfamiliar environment — Experiment 3*

Animals were subjected individually to a feeding test in an unfamiliar 7 × 3.5 m (length × width) test arena (concrete floor and 1.6 m high solid walls). Fifteen seconds after introduction of the cow into the test arena, a familiar stockperson transferred audibly and visibly 1.5 kg of concentrate feed in a bucket (phase of feed distribution). This bucket was familiar to the cows that had been trained to feed from buckets, and fixed against one of the walls of the test arena. Fifteen seconds after the cow started feeding, a 1 s air blast was delivered inside the bucket at the level of the nostrils of the feeding cow, by the aid of a tube attached to a compressor (air blast phase 1). If the cow returned feeding, after 15 s, the procedure was repeated (air blast phase 2). This test was used only for the cows of Experiment 3, and applied at the end of the experimental period, which coincided with the end of the food-deprivation period of the food-deprived animals.

#### *Social separation in an unfamiliar environment — Experiment 2*

The test was conducted in an unfamiliar 6 × 6 m (length × width) test arena (concrete floor and 2-m high solid walls). The test arena was adjacent to a 6 × 6 m pen containing pen-mates separated from the test arena by a 2 × 2 m wire mesh. The test was organised into three phases, each lasting 120 s and started as soon as the experimental cow was introduced in the test arena. In the first phase, the

**Table 2 Prediction models for heart rate at loading for the three breeds separately.**

Breed	Model	P-value of explanatory variable	% variability explained <sup>1</sup>
<b>Heart rate (bpm) at the moment of loading</b>			
Angus	137.3 – 1.5 × head raised during handling <sup>2</sup>	0.04	32.7
Blond d'Aquitaine	103.8 + 1.1 × looking at opened umbrella <sup>2</sup>	0.005	65.9
Limousin	120.6 + 4.6 × walking backwards in umbrella test <sup>2</sup>	0.02	49.7

<sup>1</sup> adjusted R<sup>2</sup>;  
<sup>2</sup> % of time.

tested animal could see its pen-mates in the waiting pen through the wire mesh. In the second, a remotely controlled curtain was automatically lowered in front of the wire mesh to prevent visual contact. In the third, the curtain was remotely opened to restore visual contact.

#### *Unfamiliar object in an unfamiliar environment in social isolation — Experiment 3*

These tests took place in a 6.5 × 6.5 m (length × width) test arena (concrete floor and 1.6 m high solid walls). During the tests, animals were video recorded. During the first phase of the reactivity test, the tested animal remained alone in the test arena during 30 s (phase of isolation). Just before the second phase, an unfamiliar object that had been hidden until that moment, was lowered from the ceiling (height: 5 m) using a rope and pulley. The animal could freely interact with the object during 60 s (novel object phase), until the object was lifted again. Phases of lowering or lifting the object took 15 s, and were excluded from the analysis. As each animal was tested twice, two novel objects were used: a 51-cm high white-and-orange traffic cone and a globular form (diameter: 30 cm) constructed from two pieces of green flexible tube (each with a length of 108 cm and diameter of 5 cm). The order of exposure was balanced for treatment and home pen.

Further details of the methods can be found in the publications of the original data (Bourguet *et al* 2010, 2011a, 2012, in prep).

#### **Interpretation of the results: towards a better understanding of stress reactions at slaughter**

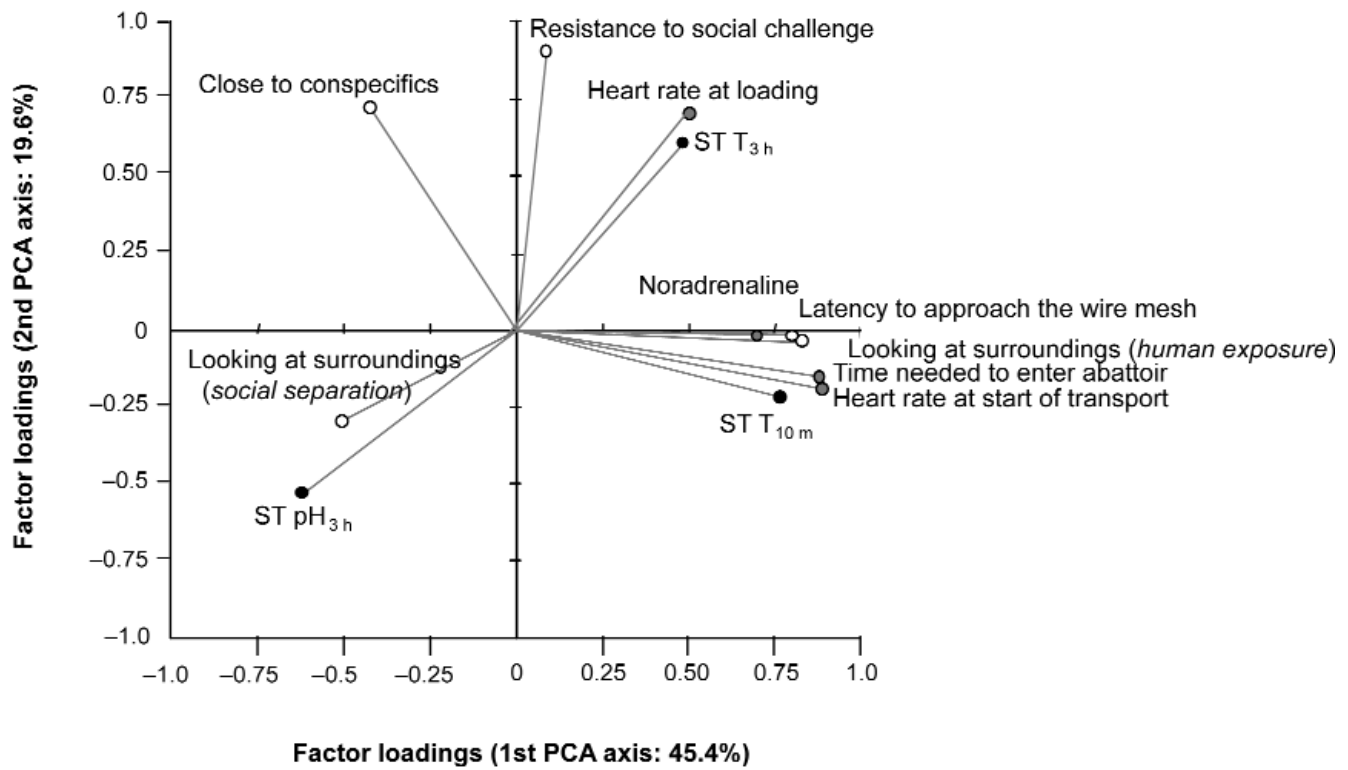
In Experiment 1 (Bourguet *et al* 2012, in prep) using young bulls, it was found that breeds differed in more than ten behaviours during the stress reactivity tests. Where differences were found, Blond d'Aquitaine bulls were more reactive than Angus, while Limousins had mostly intermediate levels. For example, Blond d'Aquitaine showed more escape attempts ( $P < 0.05$ ) and startle responses ( $P < 0.001$ ) in the surprise test, and more vigilance ( $P < 0.01$ ) in the presence of the immobile human, than Angus bulls. This is consistent with results from an earlier study in an abattoir, where Blond d'Aquitaine bulls were more reactive than Charolais bulls (Bourguet *et al* 2011b). Despite the breed differences in the stress reactivity tests, during experimental slaughter, none of the indicators of stress reactions was influenced by breed. Results did find that stress responses at

slaughter could influence post mortem muscle metabolism. Specifically, across the three breeds, heart rate at the moment of entering the abattoir was negatively correlated with pH of the *Semitendinosus* muscle, 40 min post mortem ( $r = -0.58$ ;  $P = 0.0001$ ). The correlations with early post mortem muscle pH and temperature show that as in pigs (Terlouw *et al* 2008), in bulls, stress reactions at slaughter may influence early post mortem muscle metabolism. Earlier reports on cattle have indicated that stress at slaughter may lead to less tender meat (Ferguson & Warner 2008; Gruber *et al* 2010). These results indicate further that indicators of post mortem muscle metabolism may be used as indicators of pre-slaughter stress. Finally, and most importantly, stress reactions measured during the stress reactivity tests could predict stress reactions at slaughter. Thus, bulls of the Blond d'Aquitaine, Angus and Limousin breeds that had shown relatively high heart rates after the sudden opening of the umbrella had lower pH 40 min post mortem, and thus a faster early post mortem pH decline, in the *Longissimus* muscle ( $r = -0.62$ ;  $P = 0.0001$ ). A faster pH decline is indicative of a faster muscle metabolism post mortem and probably also ante mortem, which can be explained by higher stress levels. This suggests that in these bulls, the presence of sudden events during the slaughter procedure contributed to the slaughter stress. It also shows that it is possible to identify before slaughter those individuals that are likely to be more reactive to the slaughter process. In this example, the variable indicative of slaughter stress (early post mortem pH decline) was correlated with the same explanatory variable in the three breeds (heart rate after the sudden opening of the umbrella). We found many examples where a stress indicator at slaughter was correlated with different explanatory variables, according to breed. For example, considering the bulls of the three breeds, those that had a faster heart rate during loading into the lorry before slaughter were those that showed more resistance to handling during the human exposure test or more fear reactions to the umbrella. The across-breed prediction model was significant ( $r = 0.58$ ;  $P < 0.0001$ ), but the exact relationships depended on the breed (Table 2).

In Experiment 2 on culled Normand cows, four of the activities observed in the reactivity tests showed consistent correlations with variables measured during experimental slaughter. To facilitate our understanding of relationships



Figure 1



PCA plot using correlated variables obtained during the reactivity tests and at slaughter (Experiment 2; from Bourguet *et al* 2010). See text for explanation

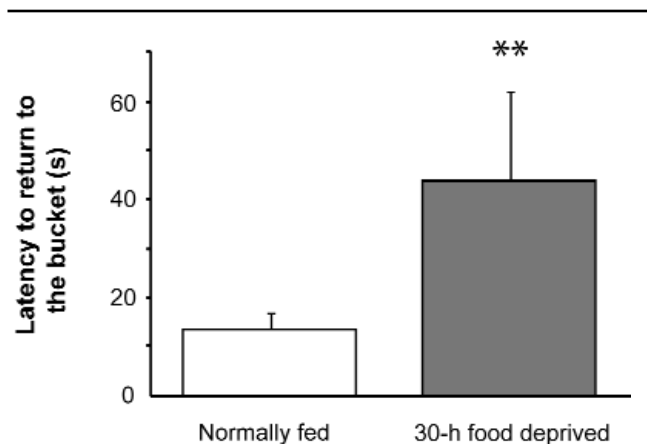
between correlated variables, they were combined in a Principal Component Analysis (Figure 1). Variables were only maintained if they had a loading on the first or second axis of at least 0.50. The first axis, explaining 45.4% of the variability, was interpreted as expressing the tendency to be fearful of unfamiliar environments or situations. It was correlated (with  $r$  values between 0.72 and 0.87) with latency to approach the wire mesh (social separation phase 1) and time spent looking at surroundings (human exposure test phase 1), time needed to enter the abattoir, heart rate during transport, urinary noradrenaline levels at slaughter and temperature of the *Semitendinosus* muscle 10 min after the start of bleeding. The second axis explained 19.6% of the variation and was interpreted as the animal's social motivation or tendency to remain close to group members. This axis was correlated with resistance to social challenge (human exposure test, phase 3;  $r = 0.92$ ) and the time spent close to conspecifics (social separation test, phase 2;  $r = 0.77$ ). Heart rate at loading, and pH and temperature of the *Semitendinosus* muscle were correlated both with the first ( $r$ -values between 0.52 and 0.64) and second axis ( $r$ -values between 0.36 and 0.67). These results are consistent with the interpretation of the axes, as loading was the moment that cows were removed from their social group and introduced into an unfamiliar environment, the lorry. Overall, results suggest that in these cows, reactivity to unfamiliarity and social disturbances were the primary

causes of stress during the experimental slaughter procedure. It is also clear from the results that cows that react more strongly to unfamiliar situations or to being removed from group members are more difficult to handle. This explains why it took more time to introduce these cows into the abattoir (correlated with axis 1) or to move them away from their pen-mates in the human exposure/social challenge test (correlated with axis 2). In this example, cows are difficult to move, not because they are fearful of humans, but because they are fearful of what humans try to make them do. The correlations with early post mortem muscle pH and temperature show that, as in pigs and bulls, in cows, stress reactions at slaughter may influence early post mortem muscle metabolism.

In experiment 3, food deprivation influenced reactivity to the sudden air-blast propelled from the bucket while the cows were feeding. Particularly after the second air blast, despite their supposedly higher food motivation, cows that had been food deprived tended to withdraw over a longer distance ( $P = 0.07$ ) they returned less quickly (Figure 2;  $P < 0.001$ ) to the bucket and consequently, spent less ( $P < 0.01$ ) time near the bucket than normally fed cows. After the first air blast, cows that had been food deprived showed more ( $P = 0.03$ ) locomotion (Bourguet *et al* 2011a).

Food deprivation or the effort treatment applied separately did not influence the reactions during exposure to the unfamiliar object or to the human, whether he was immobile or

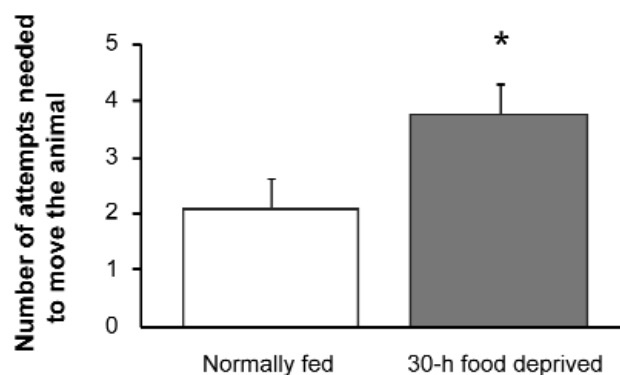
Figure 2



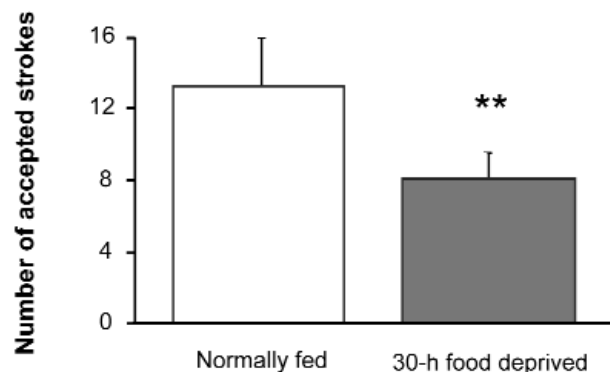
Latency to return to the food bucket after the second air blast in normally fed (white bars) and 30-h food deprived cows (grey bars; suddenness test, Experiment 3; from Bourguet *et al* 2011a).

Figure 3

(a)



(b)



Acceptance of being moved to a pre-defined pen area (top) and acceptance of strokes in heifers (bottom) of the additional effort test, either normally fed (white bars) or 30-h food deprived (grey bars; human exposure test, Experiment 3; from Bourguet *et al* 2011a).

moving or stroking the animal. However, when combined, the treatments influenced reactivity to handling. Within the group of heifers of the additional effort treatment, it took longer ( $P < 0.05$ ) time to move food-deprived heifers, and food-deprived heifers accepted strokes less easily ( $P < 0.01$ ) compared to fed heifers (Figure 3). These results show that to understand the causes of stress at slaughter, it is necessary to take into account the complexity of the slaughter environment, as the reactions to a given stressor may be exacerbated by the presence of other stressors.

In conclusion, the results show that during slaughter, aspects to which cattle may react include unfamiliarity of the situation or environment, separation from conspecifics and the occurrence of sudden events. They show also that reactivity to novelty and social separation may cause difficulties in handling. Difficulties in handling may also arise due to the combined application of food deprivation and imposed physical effort. Food deprivation may further enhance reactivity to sudden events. The above studies used simplified situations, standardised reactivity tests and experimental slaughter, to test the role of different stress factors and to a certain extent, their interactions. Further studies are needed to investigate more complex situations, containing several stressors applied simultaneously and/or successively. Finally, as in pigs, stress reactions at slaughter may accelerate post mortem muscle metabolism in cattle. Recent studies found that in cattle, stress reactions just before slaughter may influence meat quality (Gruber *et al* 2010). Further research is also needed to investigate whether a faster rate of early post mortem muscle metabolism is part of the underlying mechanism.

#### Animal welfare implications

The results obtained help us to identify those aspects of the slaughter procedure that may be particularly stressful for cattle. Results indicate further that the reactions to certain emotional stressors may increase in the presence of other stressors and that cattle may be difficult to handle due to the presence of various stressors, sometimes unrelated to the handling procedure, such as food deprivation or imposed exercise. The above experiments were not designed to have an immediate practical application with respect to slaughter procedure. However, these findings have been incorporated into training programmes for the veterinary services in charge of animal welfare in abattoirs, organised by the French Ministry of Agriculture and Fisheries in 2010 and 2011.

#### References

- Bendall JR** 1973 *Post-mortem Changes in Muscle*. Academic Press: MO, USA
- Boissy A** 1995 Fear and fearfulness in animals. *The Quarterly Review of Biology* 70: 165-191. <http://dx.doi.org/10.1086/418981>
- Boissy A and Bouissou MF** 1995 Assessment of individual differences in behavioural reactions of heifers exposed to various fear-eliciting situations. *Applied Animal Behaviour Science* 46: 17-31. [http://dx.doi.org/10.1016/0168-1591\(95\)00633-8](http://dx.doi.org/10.1016/0168-1591(95)00633-8)

- Bourguet C, Deiss V, Gobert M, Durand D, Boissy A and Terlouw EMC** 2010 Characterising the emotional reactivity of cows to understand and predict their stress reactions to the slaughter procedure. *Applied Animal Behaviour Science* 125: 9-21. <http://dx.doi.org/10.1016/j.applanim.2010.03.008>
- Bourguet C, Deiss V, Boissy A, Andanson S and Terlouw EMC** 2011a Effects of food deprivation on behavioral reactivity and physiological status in Holstein cattle. *Journal of Animal Science* 89: 3272-3285. <http://dx.doi.org/10.2527/jas.2010-3139>
- Bourguet C, Deiss V, Tannugi Cohen C and Terlouw EMC** 2011b Behavioural and physiological reactions of cattle in a commercial abattoir. Relationships with organisational aspects of the abattoir and animal characteristics. *Meat Science* 88: 158-168. <http://dx.doi.org/10.1016/j.meatsci.2010.12.017>
- Bourguet C, Deiss V, Boissy A and Terlouw EMC** 2012 Young Blond d'Aquitaine, Angus and Limousin bulls differ in emotional reactivity during tests: relationships with animal traits, stress reactions at slaughter and post-mortem muscle metabolism, in prep
- Broom DM** 1987 *Biology of Stress in Farm Animals: An Integrative Approach* pp 101-110. Springer: New York, USA. [http://dx.doi.org/10.1007/978-94-009-3339-2\\_8](http://dx.doi.org/10.1007/978-94-009-3339-2_8)
- Cockram MS, Kent JE, Jackson RE, Goddard PJ, Doherty OM, McGilp IM, Fox A, Studdert-Kennedy TC, McConnell TI and O'Riordan T** 1997 Effect of lairage during 24 h of transport on the behavioural and physiological responses of sheep. *Animal Science* 65: 391-402
- Damasio A** 2003 *Looking for Spinoza. Joy, Sorrow and the Feeling Brain*. Harcourt: CA, USA
- Dantzer R** 2002 Can farm animal welfare be understood without taking into account the issues of emotion and cognition? *Journal of Animal Science* 80: E1-E9
- Danziger N** 2006 Bases neurologiques de l'affect douloureux. *Revue Neurologique* 162: 395-399. [Title translation: Neurological basis of the emotional dimension of pain]
- Dawkins MS** 1980 *Animal Suffering*. Chapman and Hall: London, UK
- Desiré L, Boissy A and Veissier I** 2002 Emotions in farm animals: a new approach to animal welfare in applied ethology. *Behavioural Processes* 60: 165-180
- D'Souza DN, Warner RD, Dunshea FR and Leury BJ** 1998 Effect of on-farm and pre-slaughter handling of pigs on meat quality. *Australian Journal of Agricultural Research* 49: 1022-1025
- Duncan IJH** 1996 Animal welfare defined in terms of feelings. *Acta Agricultura Scandinavica, Section A. Animal Science* 27: 29-35
- Ferguson DM and Warner RD** 2008 Have we underestimated the impact of pre-slaughter stress on meat quality in ruminants? *Meat Science* 80: 12-19. <http://dx.doi.org/10.1016/j.meatsci.2008.05.004>
- Fraser D, Ritchie JSD and Fraser AF** 1975 The term 'stress' in a veterinary context. *British Veterinary Journal* 131: 653-662
- Grandin T** 1999 Safe handling of large animals. *Occupational Medicine* 14: 195-212
- Grandin T** 2006 Progress and challenges in animal handling and slaughter in the US: sentience in animals. *Applied Animal Behaviour Science* 100: 129-139. <http://dx.doi.org/10.1016/j.applanim.2006.04.016>
- Greiveldinger L, Veissier I and Boissy A** 2007 Emotional experience in sheep: Predictability of a sudden event lowers subsequent emotional responses. *Physiology and Behavior* 92: 675-683. <http://dx.doi.org/10.1016/j.physbeh.2007.05.012>
- Gruber SL, Tatum JD, Engle TE, Chapman PL, Belk KE and Smith GC** 2010 Relationships of behavioral and physiological symptoms of preslaughter stress to beef *longissimus* muscle tenderness. *Journal of Animal Science* 88: 1148-1159. <http://dx.doi.org/10.2527/jas.2009-2183>
- Horswill CA, Hickner RC, Scott JR, Costill DL and Gould D** 1990 Weight loss, dietary carbohydrate modifications, and high intensity, physical performance. *Medicine & Science in Sports & Exercise* 22: 470-476. <http://dx.doi.org/10.1249/00005768-199008000-00009>
- Jordan WP and Leaton RN** 1982 Effects of mesencephalic reticular formation lesions on habituation of startle and lick suppression responses in the rat. *Journal of Comparative Physiological Psychology* 96: 170-183. <http://dx.doi.org/10.1037/h0077880>
- Knowles TG, Brown SN, Edwards JE, Phillips AJ and Warriss PD** 1999 Effect on young calves of a one-hour feeding stop during a 19-hour road journey. *The Veterinary Record* 144: 687-692. <http://dx.doi.org/10.1136/vr.144.25.687>
- Mason JW** 1974 Specificity in the organization of neuroendocrine response profiles. In: Seemans P and Brown G (eds) *Frontiers in Neurology and Neuroscience Research* pp 68-80. University of Toronto: Toronto, Canada
- Panksepp J, Moskal JR, Panksepp JB and Kroes RA** 2002 Comparative approaches in evolutionary psychology: molecular neuroscience meets the mind. *Neuroendocrinology Letters* Dec 23, S4: 105-115
- Rosenvold K and Andersen HJ** 2003 Factors of significance for pork quality: a review. *Meat Science* 64: 219-237. [http://dx.doi.org/10.1016/S0309-1740\(02\)00186-9](http://dx.doi.org/10.1016/S0309-1740(02)00186-9)
- Terlouw C** 2005 Stress reactions at slaughter and meat quality in pigs: genetic background and prior experience: a brief review of recent findings: product quality and livestock systems. *Livestock Production Science* 94: 125-135. <http://dx.doi.org/10.1016/j.livprodsci.2004.11.032>
- Terlouw EMC, Arnould C, Auferin B, Berri C, Le Bihan-Duval E, Deiss V, Lefèvre F, Lensink BJ and Mounier L** 2008 Pre-slaughter conditions, animal stress and welfare: current status and possible future research. *Animal* 2: 1501-1517
- Terlouw EMC and Rybarczyk P** 2008. Explaining and predicting differences in meat quality through stress reactions at slaughter: the case of Large White and Duroc pigs. *Meat Science* 79: 795-805. <http://dx.doi.org/10.1016/j.meatsci.2007.11.013>
- Veissier I and Boissy A** 2007 Stress and welfare: two complementary concepts that are intrinsically related to the animal's point of view. *Physiology and Behavior* 92: 429-433. <http://dx.doi.org/10.1016/j.physbeh.2006.11.008>
- Warriss PD, Kestin SC, Brown, SN and Wilkins LJ** 1984 The time required for recovery from mixing stress in young bulls and the prevention of dark cutting beef. *Meat Science* 10: 53-68. [http://dx.doi.org/10.1016/0309-1740\(84\)90031-7](http://dx.doi.org/10.1016/0309-1740(84)90031-7)