The Old School, Brewhouse Hill, Wheathampstead,
Hertfordshire AL4 8AN, UK

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Cognitive sciences to relate ear postures to emotions in sheep

A Boissy*†, A Aubert†, L Désiré‡, L Greiveldinger§, E Delval† and I Veissier†

† INRA, UR1213 Herbivores, Site de Theix, F-63122 Saint-Genès-Champanelle, France
‡ Exploitation et Sécurité Routières, CETE Ouest, F-22015 St Brieuc Cedex, France
§ UMR UJF CNRS 5525, Acquisition, Fusion d'Information et Réseaux pour la Médecine, Technopole du Biopark, F-74160 Archamps, France
* Contact for correspondence and requests for reprints: alain.boissy@clermont.inra.fr

Abstract

Emotions are now largely recognised as a core element in animal welfare issues. However, convenient indicators to reliably infer emotions are still needed. As such, the availability of behavioural postures analogous to facial expressions in humans would be extremely valuable for animal studies of emotions. The purpose of this paper is to find out stable expressive postures in sheep and to relate these expressive postures with specific emotional contexts. In an initial experiment, we identified discrete ear postures from a comprehensive approach which integrates all theoretically distinguishable ear postures. Four main ear postures were identified: horizontal ears (P posture); ears risen up (R posture); ears pointed backward (B posture); and asymmetric posture (A posture). In a second experiment, we studied how these ear postures were affected by specific emotional states elicited by exposing sheep to experimental situations in which elementary characteristics (ie suddenness and unfamiliarity, negative contrast and controllability) were manipulated. We found that: i) the horizontal P posture corresponds to a neutral state; ii) sheep point their ears backward (B posture) when they face unfamiliar and unpleasant uncontrollable situations, hence likely to elicit fear; iii) they point their ears up (R posture) when facing similar negative situations but controllable, hence likely to elicit anger; and iv) they expressed the asymmetric A posture in very sudden situations, likely to elicit surprise. By cross-fostering psychological and ethological approaches, we are able to propose an interpretation of ear postures in sheep relative to their emotions.

Keywords: *animal welfare, behaviour, cognition, ear postures, emotions, sheep*

Introduction

The concern for animal welfare stems from the social and legal acknowledgement that animals are sentient beings, capable of feeling emotions. But, despite their central role in welfare, there is still some reluctance to ascribe emotional life to animals. However, basic (ie Darwinian) emotions, as fundamental adaptive processes, have a long evolutionary history and are shared by many species. Moreover, core components of emotions — physiological, behavioural and subjective components — have been clearly identified, and the first two components can be readily measured objectively in animal studies (Dantzer 1988). Finally, recent development in the study of emotions in animals has benefitted from merging theories and methods from psychology and ethology (Dantzer 2002; Désiré *et al* 2002). Adding to former biological theories of emotions, it is now acknowledged, since the first studies in the field of cognitive-relational theories, that emotions are the consequence of an appraisal and are therefore sustained by cognitive processes (Scherer *et al* 2001). According to Scherer (1999), an emotion results from the appraisal by the subject of a triggering situation through the assessment of a limited number of elementary characteristics (eg the suddenness, unfamiliarity and pleasantness of the situation, the ability for the subject to predict and to control the situation, etc). Recently, the behavioural and physiological responses of sheep to controlled variations of the elementary characteristics of the eliciting situation (eg suddenness, unfamiliarity, etc) were described in order to set-up the 'appraisal' framework of emotions to animals (Boissy *et al* 2007a). We showed that sheep are responsive to most appraisal characteristics defined in human studies, such as the suddenness and unfamiliarity of an event (Désiré *et al* 2004, 2006), the unpredictability (Greiveldinger *et al* 2007) and the potential control of the event (Greiveldinger *et al* 2009).

Physiological components commonly used to assess emotions in animals generally provide a quantitative assessment of the emotional activation (ie the arousal or the intensity of the emotional response) without clearly defining the exact nature of the emotion (eg the positive or negative valence of the emotional experience). For example, plasma concentrations of glucocorticoid can be increased in response to both acute negative emotional stimuli (Mason 1971) or by the expectation of a positive situation, such as the availability of a sex mate (Colborn *et al* 1991). The mobilisation of energy that precedes these situations can lead to a considerable overlap of responses to aversive and pleasant stimuli (Dawkins 1983). Likewise, common behavioural measures that generally consist of fixed action postures, such as startle, offensive or defensive postures, freezing, or approach, only provide information about the intensity of the underlying emotion (for a review see Boissy 1998). Several indicators are generally required to differentiate negative and positive emotional valence (Broom 1997; Dawkins 2001; Désiré *et al* 2002), and further behavioural indicators are nevertheless still needed to allow a convenient and reliable assessment of emotion in sheep.

In humans, expression of emotions has been extensively studied through changes in facial features. For example, one of the most popular analysis systems of facial expression in humans — the FACS (Facial Action Coding System; Ekman *et al* 1972) — is based on the description of muscular contractions (ie action units) of one's face, the combination of these action units forming a posture referring to a specific emotion. Analogous expressive or postural indicators of emotions in animals are unfortunately still missing (Berridge 2000; Boissy *et al* 2007b) but they would be highly beneficial both to scientific investigation of emotions in animals and to welfare issues, by providing convenient tools to understand and solve human-animal related concerns, for example. So far, few germinal studies have shown the availability of such parameters. For instance, facial expressions relating to gustatory sensory pleasures have been described in rats as in humans (Berridge 2003). Moreover, it has been recently shown in farm mammals that individual recognition is partly based on facial features (cattle: Coulon *et al* 2009; sheep: Kendrick *et al* 2001). Such findings call for further investigation of stable emotion-specific facial postures in farm mammals. In order to find out such facial expressions in farm animals, we focalised on ears' postures since they are essential for gathering information from the environment (Manteuffel 2006).

By contrast with other mammals, such as primates, sheep have a limited superficial facial muscles' network and thus do not appear to have a wide array of facial expressions. Nevertheless, they are characterised by a high mobility both of the neck — offering various global head postures — and of the ears, due to several muscles for rotating their ears (Nickel *et al* 1968). Do specific ear movements occur in particular emotion-eliciting contexts? Can measuring ear postures in sheep be used to accurately infer their emotions? So far, very few studies have measured the ear postures *per se* in farm mammals. Scarce reports from the literature suggest that ear postures may be useful in assessing emotional valence in farm animals. In cattle, for example, a high occurrence of pendulous ear postures was used as an indicator of the animals' positive rating of their favourite grooming sites (Schmied *et al* 2008). To our knowledge, only one study has been recently carried out on ear postures in sheep (Reefmann *et al* 2009). In that experiment, ear postures were defined *a priori* and sheep were exposed to complex situations likely to induce states of emotions but it was not possible to characterise the exact nature of the emotion induced.

The present paper focuses on the identification of ear postures and their possible link with emotional states in sheep. In an initial experiment, we identified discrete ear postures from a comprehensive approach which distinguish all theoretically measurable ear postures without *a priori* interpretations. In a second phase, we ran three experiments in order to explore the possible correspondence between previously identified discrete ear postures and emotions. According to the appraisal framework of emotions previously used in sheep (Désiré *et al* 2002; Boissy *et al* 2007a), ewes were individually exposed to triggering situations varying in their degree of either suddenness or unfamiliarity, and of negative contrast or controllability.

Materials and methods

An initial experiment was conducted to identify discrete ear postures. In a second experiment, three groups of sheep have been utilised separately to specifically assess the relationship between the identified discrete ear postures and three elementary components of emotions corresponding to: (i) suddenness and familiarity of a visual event (Study 1); (ii) negative contrast (ie, the drastic reduction of a food reward (Study 2); and (iii) control (ie control of the access to a food reward) (Study 3).

Animals and rearing

Ewes from the Romane breed, aged between six and ten months, were used; ten for Experiment 1 and 78 for Experiment 2 (32, 22, 24 in Studies 1, 2, 3). They had been separated from their dam 24 to 48 h after birth and housed with other animals of the same age. At the time of the experiments, the ewes were reared in large pens (called home pens, 3.8 m^2 per animal) with deep-litter straw bedding, adjacent to an experimental chamber (Figure 1). They were provided hay *ad libitum* and 400 g of food pellets composed of barley, sugarbeet, wheat, maize, sunflower and soya (Thivat Nutrition Animale, Cusset, France). The food was distributed daily at 1700h in the home pen. When the training procedure started (see below), the ewes received food pellets during tests and were supplemented with pellets in their home pen to reach a total provision of 400 g.

Experimental set-up

The experimental chamber was divided into three compartments: a pre-test (1.5 m^2), a test arena (3 m^2) and a corridor (1.8 m^2). Each compartment was delineated by 1.8-m high wooden partitions that prevented animals from seeing each other (Figure 1). Sliding doors permitted access from one compartment to the next. A device for delivering food pellets was placed in the test arena at the opposite side to the entrance. It consisted of a deck 30 cm above floor level with a central aperture housing an adjustable 15-cm diameter trough. Food pellets were delivered in the trough via an electronic system placed outside the arena and that could be controlled by the experimenter.

Four video cameras (three Sony SPT-MC128CE and one Sony DCR-TRV 320E Digital Handycam, Sony Corporation, Tokyo, Japan) were used to record the behavioural reactions and postures of the lambs around the trough in the test arena. The cameras were connected to a video recorder that simultaneously recorded the images from the four cameras on the same tape (Sony SVT-1000P, Sony Corporation, Tokyo, Japan) thanks to a quadravision system (MV25 Multivision Processor, model MX25, Robot Research, San Diego, California, USA). The cameras were placed in such a way as to provide top, side and face-on views of the ewes.

Procedures

The procedures to train and test the animals have already been published (Désiré *et al* 2004, 2006; Greiveldinger *et al* 2007, 2009, 2010). We will only summarise them briefly in the present paper.

General training procedure for ewes

To accustom the animals to the experimental chamber, they were given free access to the chamber from their home pen for one or two weeks; all access doors were opened and food pellets were at their disposal in the test arena. Then, once they accepted to feed in test arena, each ewe was individually exposed to the chamber; the access doors were shut when she moved from one compartment to the next one. This was repeated on at least five sessions. After this training phase, each ewe was exposed to test procedures specific to each study.

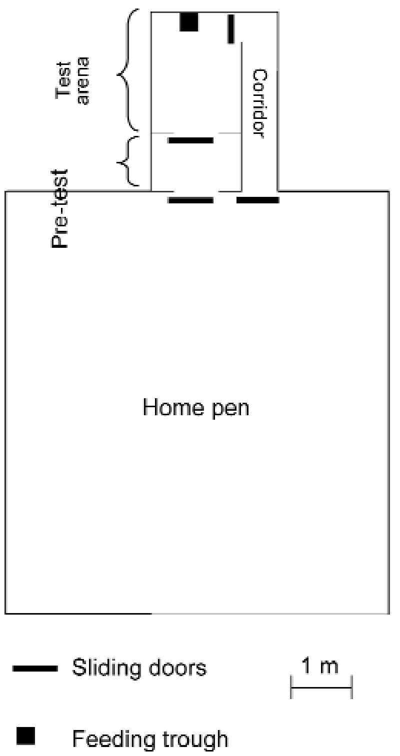
Specific procedures for testing ewes

In Experiment 1, a rope-and-pulley device installed behind the trough of the test arena was utilised to move a white scarf (0.2 × 0.2 m; length × breadth) from a non-visible location to 0.2 m above the trough in full sight of the animal. While the ewe was eating, the scarf was moved by the experimenter at a speed of 0.88 m s^{-1}. The ewe was left two minutes more in the arena. The test was repeated once daily on three consecutive days.

In Experiment 2, Study 1, the rope-and-pulley device was used, as in Experiment 1, with the exception that a second object could be used (a flat square made of the same white textile as the scarf). During training, half the ewes were familiarised with the scarf and half with the flat square; these objects always appeared slowly (0.06 cm s^{-1}). The ewes were trained once daily until they did not step back when the object appeared for three consecutive days. Then, during tests, only the scarf was presented (it was thus familiar for certain ewes and not so for others). It was moved down next to the trough either slowly as previously (0.06 cm s^{-1}) or rapidly (0.88 m s^{-1}). Four test sessions were run.

In Experiment 2, Study 2, the ewes were trained to perform an operant task (to cross a beam with their muzzle) to get a large food reward (50 g food pellets) or a small food reward (10 g food pellets). The photobeam and two photoelectric cells were placed in a 0.2 × 0.2 × 0.2 m (length × breadth × height) hole placed in

Figure 1



Experimental set-up (top) and the scarf (bottom) used for the two experiments (except for Studies 2 and 3).

the partition, 1 m from the left-hand side of the trough. Each ewe was subjected to one session a day and the session was terminated when she had eaten four rewards, which took between 2 and 4 min. After ten days of training the animals were subjected to three test sessions with the same conditions, then for the next three sessions the ewes trained with a large reward and received a small one (negative contrast), while the remaining ewes continued to receive a small reward (no contrast).

In Experiment 2, Study 3, food was always present in the trough of the test arena but the animals did not have free access to it. From time-to-time during a session, an air blower was turned on above the trough and a grid was moved above the trough to prevent animals from eating. Half the ewes were trained to perform the same operant task as in Study 2 (crossing the photobeam) in order to resume access to the food (air blower is turned off and the grid is removed). The remaining ewes were yoked to the previous ones: they received exactly the same access to the food but without controlling it. Ewes that could control access to the food and their yoked counterparts were further observed during four test sessions, once the former had acquired the operant task.

Identification and detection of ear postures

Video recordings were taken during the following sessions.

Experiment 1 — we selected a total of ten recordings that allow full vision of the animals; these were taken during the first, second, or third session where the scarf was presented to animals and recordings from 30 s before to 30 s after the appearance of the scarf were analysed.

Experiment 2, Study 1 — recordings from 30 s before to 30 s after the appearance of the scarf during the four test sessions.

Experiment 2, Study 2 — recordings from 10 s before to 10 s after delivery of the food reward during the three test sessions.

Experiment 2, Study 3 — recordings from 5 s before to 5 s after the air blower was turned on during the four test sessions.

Observer Video Pro (version 4.0.21, Noldus Information Technology, The Netherlands) was used to record all ear postures irrespective of the experiment. In Experiment 1, two independent observers noted all changes in the position of ears according to two criteria: the position of the ear in regard to the frontal plane of the head, and the visibility of the auricle. Within each criterion categories were exclusive (see Figure 2):

• Position of the ear in the frontal plane — the ears can be aligned with frontal plane, oriented forward (the top of the ear is in front of the frontal plane), oriented backward (the top of the ear is behind the frontal plane), or asymmetric (the two ears differ in their position in regard to the frontal plane);

• Visibility of the auricle — the auricles can be flat (the inner and outer sides are not visible, the inner side is parallel to the floor, the observer can see the full ears), open (the inner sides are visible by an observer placed in front of the animal), closed (the inner sides are not visible, the outer sides are visible at the root of the ear, the ears cannot be fully seen by the observer), asymmetric (one inner side visible, one not).

The positions of ears in the frontal plane of the head were recorded separately from the positions of ears according to the visibility of the auricle. Table 1 presents the 16 theoretical combinations obtained from the crossing of the 4 × 4 framework (four in the frontal plane and four facial views for the visibility of the auricle). From the 16 combinations of position of the ears, we identified four discrete ear postures (see results from Experiment 1). These defined postures were further encoded in all studies of Experiment 2.

Statistical analysis

We used the software SAS (version 8.1, SAS Institute Inc, Cary, NC, USA) for all analyses. In Experiment 1, each time an observer noted a change in ear position, we checked the position that the other observer noted. We calculated the frequency and the duration of each of the 256 possible associations between the 16 combinations of ear positions from Observer 1 and those from Observer 2. The consistency between the two observers encoding the ear postures was assessed with Cronbach alpha index.

In Experiment 2, the duration of ear postures was arcsine-transformed and compared between conditions with a mixed model of variance analysis for repeated measures. Repetitions were for session number and time during a session (before vs after the event). The correlation matrix was considered unstructured. The results are expressed as mean (± SD). The limit of significance was set at $P < 0.05$.

Results

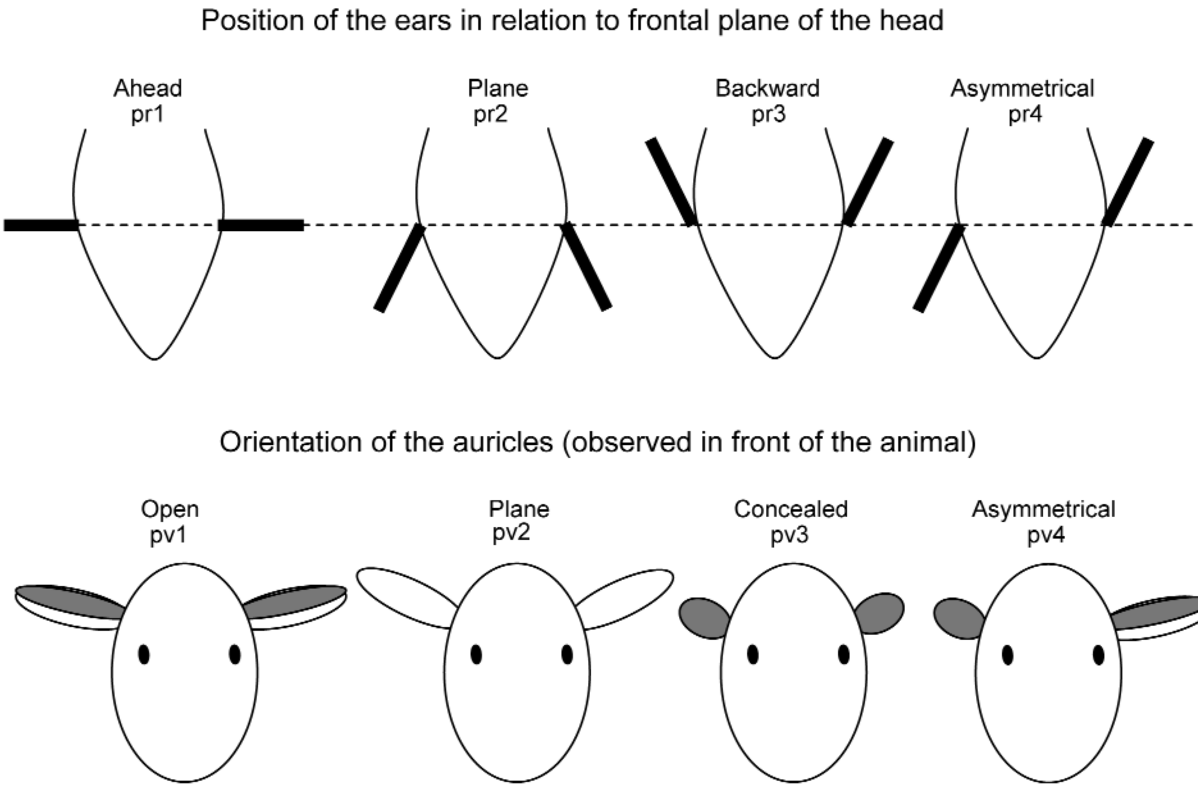
Experiment 1 — Identification of discrete ear postures

The consistency between observers encoding the ear postures was high (Cronbach's alpha = 0.8645). The observations were then considered reliable. Figure 3 shows the frequency and mean duration of the 16 theoretical combinations of ear positions determined from the frontal plane and visibility of the auricle. Certain combinations were never observed (ie combinations 5, 9, 10, 12 and 13, such as ears oriented forward and flat auricles). Some other combinations (ie combinations 3, 4, 7, 8, 14, 15) were displayed for very brief periods (mean duration < 1 s).

The remaining combinations were frequently expressed (combinations 1, 2, 6, 11 and 16), with significant mean durations (ie > confidence interval of mean). These combinations were therefore considered as distinctive and meaningful ear postures. In addition, it was decided to regroup postures 1 and 2 (the two ears are either ahead or in the frontal plane with visible auricle) since they were closely associated during the longest expressive episodes. Finally, four discrete ear postures were considered for further analysis:

• 'Raised ears' posture (R posture), which correspond to combinations 1 and 2. The two ears are in the same position relative to the frontal plane (either ahead or aligned), and auricles are visible from front view.

Figure 2



Position of ears collected from ewes according to two criteria: position of the ears in relation to frontal plane of the head (top) and orientation of the auricles observed in front of the animal (bottom).

Table 1 Labels of the 16 theoretical combinations between the position of the ears in the frontal plane of the head and the orientation of the auricles observed in front of the animal.

		Front view			
		pv1	**pv2**	**pv3**	**pv4**
View from above	**pr1**	1, pr1pv1	5, pr1pv2	9, pr1pv3	13, pr1pv4
	pr2	2, pr2pv1	6, pr2pv2	10, pr2pv3	14, pr2pv4
	pr3	3, pr3pv1	7, pr3pv2	11, pr3pv3	15, pr3pv4
	pr4	4, pr4pv1	8, pr2pv2	12, pr4pv3	16, pr4pv4

• 'Ears in the plane' posture (P posture), which corresponds to combination 6. The two ears are in the frontal plane and auricles are concealed from front view'.

• 'Ears backward' posture (B posture), which corresponds to combination 11. The two ears are behind the frontal plane and auricles are concealed from front view.

• 'Asymmetrical ears' posture (A posture), which correspond to combination 16. The two ears are in two distinct positions relative to the frontal and visibility of auricles is asymmetrical.

Regarding the combinations displaying for very brief periods, they could correspond to transitional postures between two of these four ear postures. Each of the transitional postures was then considered as belonging to the same defined posture to which it was associated most often: combination 3 was then regrouped with posture R, combinations 4, 8 and 14 were regrouped with posture A, and combinations 7 and 15 were regrouped with posture B.

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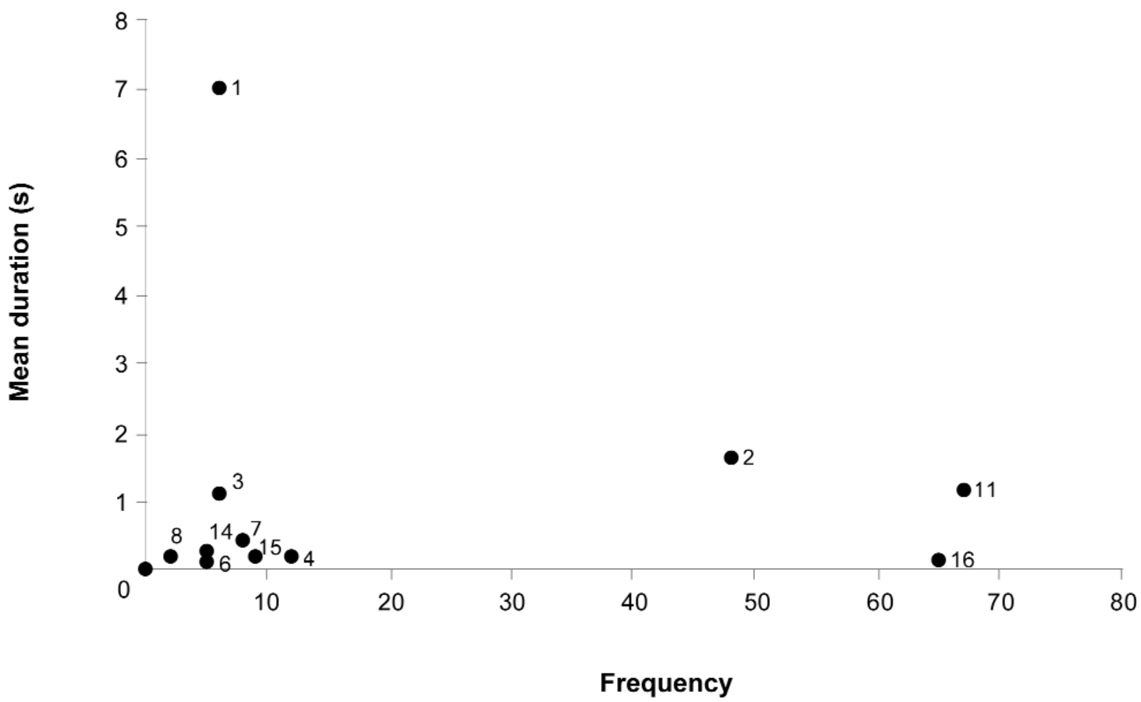
Table 2 Duration (s) spent in ears' postures by the ewes exposed to a neutral, a sudden or an unfamiliar event (Experiment 2, Study 1, n = 32).

	Ears in the plane (P)	Ears backward (B)	Asymmetric ears (A)	Ears raised (R)	SEM	*F*-value	*P*-value
Session 1							
Neutral	20.3[a]	1.0[c]	4.2[b]	3.1[bc]	2.5	6.43	0.01
Sudden	16.8[a]	1.2[d]	8.1[b]	4.5[c]	2.8	5.23	0.01
Unfamiliar	8.3[a]	5.3[c]	5.0[c]	12.2[b]	1.7	3.52	0.05
Sessions 2-4							
Neutral	24.5[a]	0.8[c]	2.1[b]	3.1[b]	3.2	5.56	0.01
Sudden	19.2[a]	0.9[d]	7.1[b]	4.0[bc]	3.3	3.23	0.05
Unfamiliar	22.0[a]	0.5[c]	3.4[b]	4.2[b]	2.8	3.74	0.05

Figure 3



Distribution of frequency and mean duration of combinations observed for fear postures. Each label indicates a specific combination (cf Table 1). Combinations that were never observed (ie 0 values) are combinations 5, 9, 10, 12 and 13.

Experiment 2 — Assessing stable relations between ear postures and emotional contexts

Study 1 — Suddenness/unfamiliarity

Whatever the session, the ears were mainly in the plane posture before the appearance of the scarf (21.2 [± 3.2] vs 2.4 [± 2.1] s, 0.7 [± 0.3] and 4.8 [± 4.3] s for ear in the plane, raised ears, asymmetric ears and ears backward; $F = 18.4$, $P < 0.001$).

The ear postures changed when the scarf appeared. The change depended on the speed of the presentation and the object used for training (Table 2). In response to the rapid appearance of the scarf, the ewes spent more time in the asymmetric ear posture. Although the time spent in this posture decreased during subsequent sessions, it was always significantly higher than the time spent in the other ear postures, except the posture with the ears in the plane.

In response to the slow appearance of the scarf in the first session, the ewes that had been trained with the square spent more time with the ears raised or backward while the time spent with the ears in the plane was decreased. From the second to the fourth session, their time spent with the ears raised decreased whereas their time with the ears in the plane increased.

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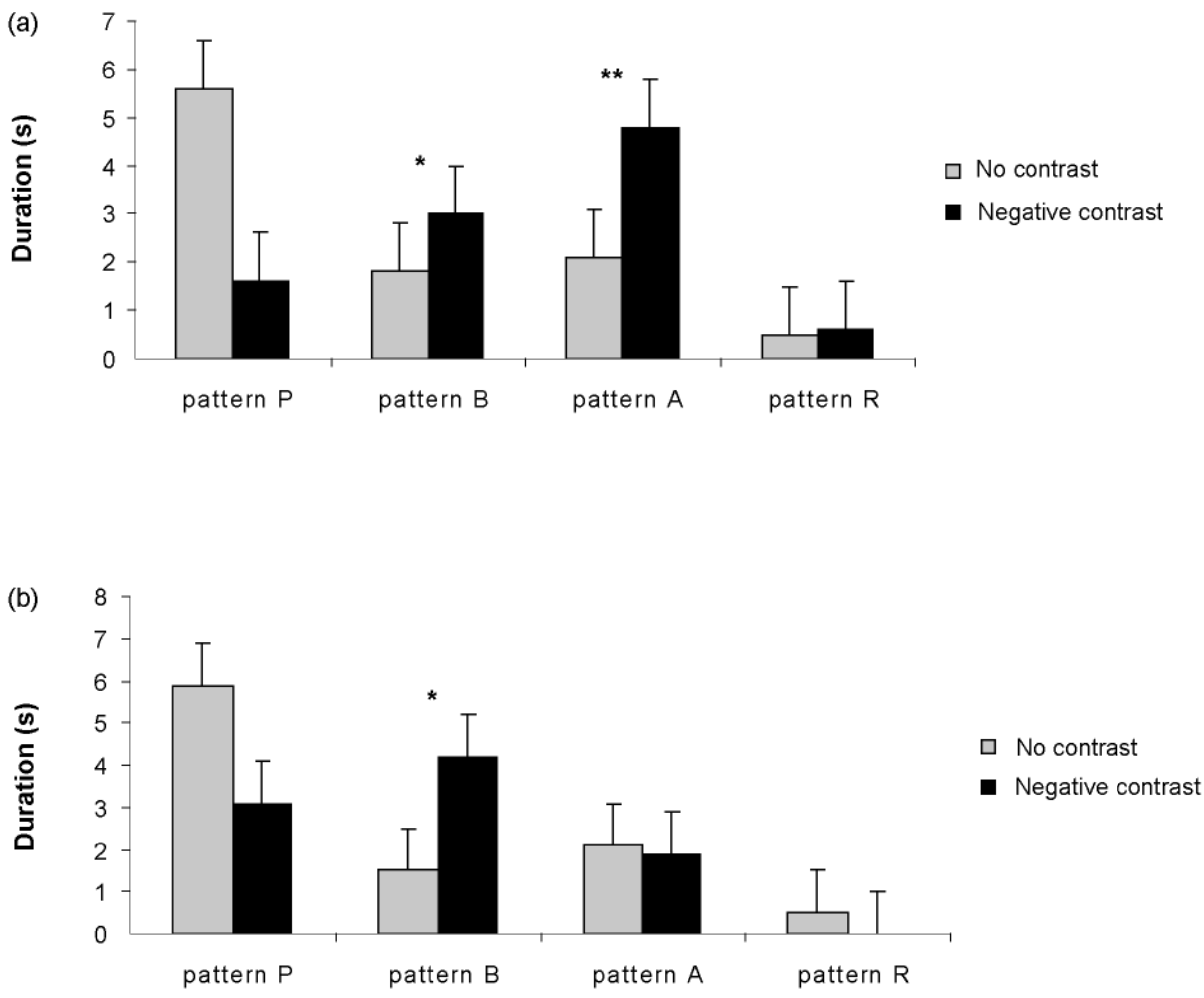
Figure 4



Time duration (s) spent in ears' postures by the ewes exposed to a negative contrast during (a) the first session and (b) the following two sessions (Experiment 2, Study 2, n = 22). Half of the ewes that were previously trained with a large reward of food received a small one (negative contrast) while the other half continued to receive a small reward as during training (no contrast). Four main ear postures were identified: horizontal ears (pattern P), ears pointed backward (pattern B), asymmetric posture (pattern A) and ears rose up (pattern R). * $P < 0.05$; ** $P < 0.01$.

The ewes that had been trained with the scarf (ie same object as for the test) did not show a change of ear posture from before to after the slow appearance of the scarf. The time spent with the ears in the plane was higher than the time spent in the other ear postures (Table 2). This difference was still significant for the next three sessions.

With the exception of the first session, the ewes spent very little time with their ears backward after the appearance of the scarf and this did not vary with treatments.

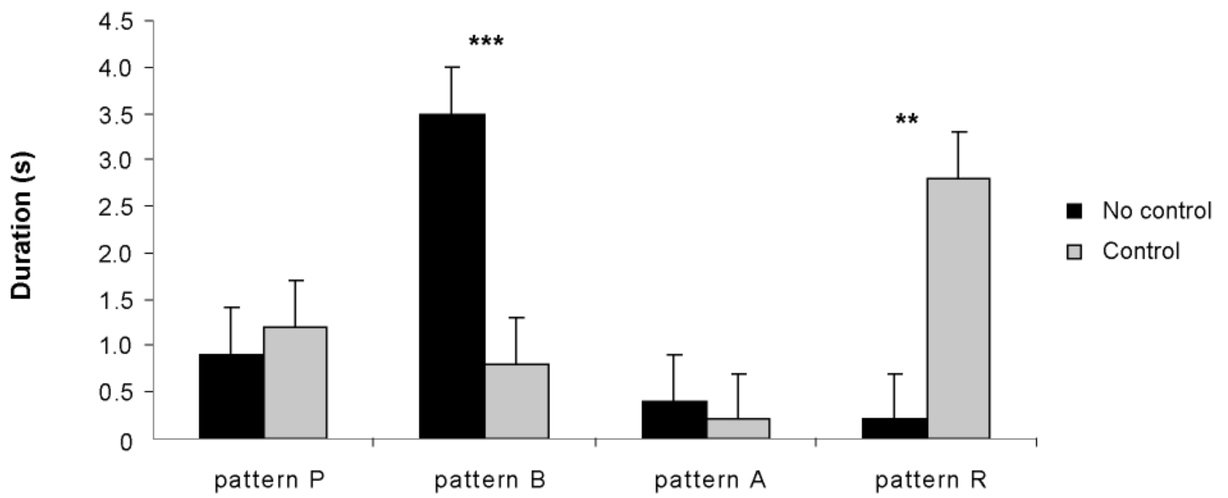
Study 2 — Negative contrast

The ewes were particularly sensitive to the shift in the size of the reward (Figure 4). Compared to ewes that had always received a small reward, those that were shifted from a large to a small reward (ie negative contrast) spent more time with their ears asymmetric ($F = 4.5$, $P < 0.01$) or oriented backward ($F = 3.2$, $P < 0.05$) at the time when the reward was delivered. For the next two sessions, the difference between the two treatments was significant only regarding the posture with the ears backward ($F = 2.9$, $P < 0.05$).

Study 3 — Control

When the ewes were eating, their ears were mainly in the plane (10.5 [± 3.5], 1.3 [± 1.1], 2.7 [± 1.3] and 0.9 [± 0.6] s for the time spent with ears in the plane, ears raised, asymmetric ears, and ears backward; $F = 8.3$, $P < 0.001$). The possibility to control the situation elicited different ear postures when the air blow was initiated (Figure 5): the ewes that could interrupt the air blow raised their ears for longer ($F = 4.9$, $P < 0.01$) and oriented them backwards less often ($F = 8.3$, $P < 0.001$) than the ewes that had no control over the situation.

Figure 5



Time duration (s) spent in ears' postures by the ewes controlling or not the access of food (Experiment 2, Study 3, n = 26). Ewes that were previously trained to control throughout the experiment the interruption of air flow and the access of food are compared to yoked ewes that had no possibility to control the accesses to food. Four main ear postures were identified: horizontal ears (pattern P), ears pointed backward (pattern B), asymmetric posture (pattern A) and ears rose up (pattern R). ** $P < 0.01$; *** $P < 0.001$.

Discussion

The present study aimed to identify specific emotion-related ear postures in sheep. First, we objectively identified four discrete ear postures: ears in the plane (the two ears are in the frontal plane and auricles are concealed from frontal view), ears raised (the two ears are either ahead or aligned and auricles are visible from front view), ears oriented backward (the two ears are behind the frontal plane and auricles are concealed from front view), and asymmetric ears (the two ears are in two distinct positions relative to the frontal and visibility of auricles is asymmetrical). From the pool of putative combinations, some combinations were never observed; this is easily understandable since they represent anatomically irrelevant postures. For instance, combination 5 would correspond to ear ahead in the frontal plane but with auricles facing the ground. Then, we analysed the occurrences of these four discrete postures in relation to specific experimental situations defined according to elementary appraisal components that were previously shown as being relevant for eliciting emotional responses in sheep: suddenness, unfamiliarity, negative contrast, and uncontrollability. We observed that: i) the posture with the ears in the plane was mainly associated with neutral situations; ii) the backward posture was associated with unfamiliar and uncontrollable unpleasant situations; iii) the posture with raised ears was specifically displayed in response to an unfamiliar, unpleasant but controllable situation; and iv) the asymmetric posture is mainly displayed in sheep exposed to sudden situations.

The two postures representing raised ears (ie forward ears) and asymmetric ears have already been reported by Reefmann *et al* (2009) as increasing during social contexts eliciting negative emotions. Nevertheless, in our current experiments, we could link these specific ear postures with specific emotional experiences by exposing animals to experimental situations defined according to the cognitive components sheep use to evaluate their environment (Désiré *et al* 2002; Boissy *et al* 2007a; Veissier *et al* 2009). In addition, the comparison between our results and what was found in humans can help the interpretation of sheep ear postures. For instance, the facial expression of emotions triggered by unfamiliarity in humans is described by lowered eyebrows and raised eyelid (Kaiser & Wehrle 2001). Interestingly, the muscle network implied in lowering eyebrows in humans would be evolutionarily related to the muscles controlling the mobility of the ears in animals (Fridlund 1994). The contraction of homologous muscles could be therefore responsible for the lowering of eyebrows in humans and raising of ears in animals. Since eyebrows play a major role in expressing emotions in humans (Ekman *et al* 1972), emotions in farm mammals may be reflected in their ear postures.

Most of the results reported here were obtained in situations with a negative valence for the animals. According to Fraser and Duncan (1998), different evolutionary processes seem to have selected negative from positive emotions. Negative emotions are supposed to have evolved in 'need situations', such as a threat to survival or reproductive success, whereas positive emotions are supposed to have generally evolved in 'opportunity situations' where the resulting action may enhance individual fitness without being essential for it (Boissy *et al* 2007b). This may be the reason why positive

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emotions are more variable (either inter- or intra-individuals) and versatile, hence more difficult to approach than negative emotions. Relating to the homology between muscles involved in lowering eyebrows in humans and in animals' ears raising (Fridlund 1994), the previous results would indicate that some negative emotional experiences involve rising ears up whereas positive emotional experiences could coincide with non-erect ears (in our study the plane ear posture). Further research is thus needed on the positive side of the emotional scale to attempt to identify specific facial expressions as it is known in humans. For example, asymmetry of ear postures may differ between negative and positive emotional states, due to lateralised behaviour (Quaranta *et al* 2007) thought to result from contra-lateral hemispheric brain activity (Wager *et al* 2003).

From our previous studies and according to the framework used by Sander *et al* (2005), sheep appear to have the potential to feel a wide range of emotions, including fear, anger, rage and despair, because they use the same appraisal components involved in such emotions as in humans (Boissy *et al* 2007a; Veissier *et al* 2009). For instance, despair in humans is triggered by situations which are evaluated as sudden, unfamiliar, unpredictable, discrepant from expectations, and uncontrollable, whereas boredom results from an overly predictable environment, and all these components have been found to affect emotional responses in sheep. Since it has been shown in the present study that ear postures are related to specific appraisal components, these defined ear postures could represent specific emotional signatures in sheep. Thus, the backward posture that is associated with unfamiliar and uncontrollable unpleasant situations would express fear. The raised ear posture that is displayed in response to an unfamiliar but controllable unpleasant situation would characterise anger. Finally, the asymmetric ear posture that is mainly displayed in response to sudden situations in relation with a startle response would express surprise. The assertions described in this study are not so far from the intuitive knowledge of breeders or other people who have close relations with animals (and sheep in this case). The present paper gives support to this intuitive interpretation of animal expressions.

Our interpretation of ear postures in sheep from a quantitative ethogram-based approach could be reinforced by analysing the concordance with the Qualitative Behaviour Assessment (Wemesfelder 2001), that is a method based upon the integration by observers of perceived animal behaviour expression, using descriptors such as 'calm', 'aggressive', 'sociable' or 'indifferent'. This method, based on the body language of animals, has been recently validated for sheep (Wickham *et al* 2009). Moreover, the description of emotion-specific expressions in sheep provides further information to better understand the social function of emotions. Indeed, emotions are sustained by three main processes: physiological (ie somatic and visceral changes), subjective (ie the mental and representational content that can be verbally described in humans), and expressive (ie the visible changes in behaviour, postures, gestures and expressions). It has been shown that the expressive component of emotions are fundamental for many social processes. This has been demonstrated not only in humans, but also in other primates (Dantzer 1988). However, little work has been done on other animals, such as farm species. It has been recently shown that such animals (eg cattle or sheep) use facial information to recognise specific individuals (Kendrick *et al* 2001; Coulon *et al* 2009). Hence, such animals are sensitive not only to the presence vs absence of conspecifics, but also to subtle physical features of specific social partners. Our study shows that sheep express specific stable changes in their facial appearance (ie ear postures). These changes could provide relevant information to conspecifics about their environment. Further studies should be done to test such a hypothesis, ie using conditioning procedures, and to test whether animals are able not only to recognise conspecifics' identity but also to identify their emotional state throughout their ear postures.

As we already claimed in previous papers, by applying models developed for humans, we increase the knowledge on how animals understand their environment and the likely emotions they can feel. Moreover, such a non-invasive and convenient method with freely moving animals should help to better interpret what animals experience as unpleasant in their housing environments. It should establish the basis for understanding and then improving current housing and husbandry conditions from an animal's point of view. Such findings from sheep on how to assess emotional states may be readily transferable to closely related prey species at the very least.

In conclusion, this study provides some insight into emotional expressions in sheep. This constitutes a first step to characterise specific emotion-related facial expressions in farm animals. Observations of ear postures are a reliable non-invasive method for assessing the valence of emotional states in sheep. We found that: i) sheep point their ears backward when they face unfamiliar, unpleasant, and uncontrollable situations, hence likely to elicit fear; ii) they point their ears up when facing a similar negative situation but controllable, hence likely to elicit anger or at least some preparation of an active response; and iii) their ears are more often asymmetric in very sudden situations, likely to elicit surprise. These findings need to be confirmed in other situations that might be appraised similarly by sheep but using different stimuli. It is necessary to extend these first four expressive postures characterising neutral or negative emotions (ie fear, anger and surprise) to take into account positive emotions in animals.

Animal welfare implications

The interpretation of ear postures could be used to assess farming practices from the viewpoint of animals. It could also help to understand what a given animal is feeling at a certain time and the subsequent behaviour it is likely to adopt, eg flight when the ears are oriented backward or attack when they are raised up. These specific emotion-related facial expressions could be easily used to enrich the behavioural measurements for an overall assessment of welfare at farm level.

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