Methodologies to measure affective states in animals: a focus on cognitive approaches

Dr Else Verbeek
Dr Caroline Lee
CSIRO livestock Industries
FD McMaster Research Laboratories
Armidale, NSW, Australia

Abstract

In recent decades, a number of different studies have shown that animals can experience pain and distress. The acknowledgement that animals have the ability to experience basic emotions has led to the question: can animals also experience a wider range of pleasant and unpleasant states (also called affective states)? However, studying affective states in animals is difficult due to the subjective nature of such states. Despite this, novel cognitive approaches to objectively measure affective states have been developed in recent years.

Introduction

Over the last three decades, there has been an increased interest in the welfare of animals that are used for food production and in scientific research. There is a general concern that animals may suffer when kept in impoverished environments or when exposed to stressful and painful situations. This has led to a substantial amount of research on animal welfare, and it is now commonly accepted that mammals can experience pain and distress (for overview see Broom 1991; Dawkins 2008). The discovery of basic experiences such as pain and distress has now opened up a new field of research in which the ability of animals to feel a range of different affective states – defined as states that are pleasant or unpleasant rather than hedonically neutral – are being explored (Duncan 2006; Fraser 2009). The majority of this research has focused on negative affective states while positive ones have received relatively little attention. Despite the lack of attention to positive states, it has been suggested that they are important for the welfare of animals (Boissy et al. 2007). Therefore, there is a need to develop measures that can assess positive experiences in animals. The aim of this paper is to discuss methodologies that are currently available or being developed in animal welfare science to objectively measure affective states in animals.

Behavioural and physiological measures

There is a wealth of evidence showing that certain husbandry procedures can lead to signs of pain and distress in animals. For example, social isolation in sheep leads to increased plasma cortisol concentrations, plasma osmolality and haematocrit values indicating stress (Parrott et al. 1988; Hernandez et al. 2010). In addition, isolated sheep show repeated attempts to escape and increased vocalisations and activity (Parrott et al. 1988; Apple et al. 1993; Vandenheede & Bouissou 1993; Hernandez et al. 2010). Another example is castration without anaesthesia or analgesics, which leads to several physiological and behavioural signs of stress, such as increased plasma cortisol concentrations, reduced activity and food intake, stiffness, scratching, increased vocalisations and abnormal body postures in lambs (Mellema et al. 2006; Melches et al. 2007), piglets (Hay et al. 2003; Leidig et al. 2009) and calves (Molony et al.

1995). Behavioural and physiological measures have therefore provided much insight into the subjective experiences of animals exposed to pain and stress.

However, there is limited research on the behavioural and physiological indicators of positive affective states. The most studied potential indicator of positive affective states is play behaviour in young animals. Young animals play when housed in comfortable, social and familiar environments with sufficient space available (Vanderschuren et al. 1995; Jensen et al. 1998; Jensen & Kyhn 2000), but not when sick, injured or hungry (Held & Spinka 2011). Young rats find play behaviour positively rewarding and will press a lever many times to be tickled by the experimenter (Burgdorf & Panksepp 2001). These results suggest that the expression of play behaviour could be an indicator of a positive affective state. Other potential indicators of positive affective states are ear postures in adult sheep. Sheep being voluntarily groomed by a human experimenter showed fewer ear posture changes, more axial and fewer forward ear postures accompanied by high heart rate variability, an indication of reduced stress (Reefmann et al. 2009b). Furthermore, voluntarily groomed sheep kept in a barren environment showed higher amplitude changes in cortical haemoglobin concentrations compared to groomed sheep in an enriched environment, possibly because the contrast between the negative housing environment and the positive stimulus was larger (Muehlemann et al. 2011). In contrast, sheep ear postures could also be a potential indicator of negative affective states: separation from the flock mates resulted in a high number of forward ear postures and a high frequency of ear posture changes (Reefmann et al. 2009a). Therefore, sheep ear postures may be indicative of their affective state. Finally, vocalisations could also be an indicator of positive affect; low-pitched bleats in ewes while licking and nursing lambs (Sèbe et al. 2010) and 50 kHz vocalisations in rats during play (Burgdorf & Panksepp 2001) could potentially be interpreted as expressions of positive affect.

Although behavioural and physiological measures of pain and pleasure are very useful, their interpretation is not always straightforward. For example, plasma cortisol concentrations are not only increased during stressful situations, but also when animals are anticipating a food reward or during other emotionally arousing situations (Rushen 1991; Mormède et al. 2007). Cortisol concentrations can therefore be increased during both negative and positive affect situations and may be an indicator of arousal rather than the affective state. Furthermore, fear responses may differ between individual animals and some may cope with a stressor in an active way, while others may show a more passive response (Erhard & Mendl 1999). Play behaviour also varies considerably between species, flocks, males and females and individual animals (Held & Spinka 2011). Therefore, measures of behaviour and physiology can be interpreted in different (and potentially contradicting) ways. Because of such difficulties, alternative methods that aim to find more direct measures of affective states would be valuable.

Cognition and affective states

The major obstacle in assessing affective states in animals is that affective states are subjective experiences and therefore extremely difficult to measure. Even in humans, the easiest way to find out how someone "feels" is by verbal communication. However, that does not mean that animals (or humans) that are unable to verbally communicate their feelings do not experience them. There are alternative ways that can also provide insights into an individual's affective state. Such methods originate from the field of human psychology and explore the link between affective states and cognition. Cognition is defined as the mechanisms by which human and non-human animals acquire, process, store and act on information from the environment (Shettleworth 1998). A cognitive process is required to assign "value" to a stimulus, or in other words, to determine whether a stimulus (e.g., event or object) is more or less desirable (Friston et al. 1994; Dolan 2002). For example, a stimulus needs to be identified as potentially threatening in order to induce fear. Such cognitive processes are likely to be evolutionarily adaptive because they help the animal to decide what situations to avoid and where to seek rewards (Panksepp 2005).

The link between cognition and affective states is two-directional. Not only can cognitive processes influence the affective state, but human psychological studies have also found that a change in affective state can alter cognitive processing. For example, a positive mood can enhance creative problem-solving tasks, the recollection of memory details and increase performance at unusual word association tasks (Isen et al. 1985; Isen et al. 1988; Ashby et al. 1999; Dolcos et al. 2004). The existence of strong links between cognition and affective states in humans leads to the question whether such links also exist in animals. There is a possibility that experimental manipulations of animals' affective states could also lead to changes in cognitive processing. Changes in cognitive processing could be accurate and objective measures of subjective affective states, and may therefore provide a starting point for the measurement of subjective affective experiences in animals.

Cognitive biases

In 2004, Harding et al. (2004) developed a methodology to measure changes in cognitive processes after a change in affective state in rats. More specifically, their methodology aimed to measure a judgement bias. A judgement bias occurs when an individual expresses a negative (or positive) rather than neutral judgement bias of ambiguous stimuli depending on the affective state. For example, anxious and depressed people tend to interpret events more negatively and judge ambiguous stimuli unfavourably compared to non-depressed individuals (MacLeod & Byrne 1996; Amin et al. 1998; Gotlib & Krasnoperova 1998; Strunk & Adler 2009). People diagnosed with clinical depression also tend to show a reduced anticipation for positive events (Haaga & Beck 1995). In the experiment by Harding et al. (2004), rats were trained to press a lever in response to an auditory tone associated with a positive event (food reward) and to refrain from pressing the lever when they heard a different tone associated with a negative event (white noise). Rats were then exposed to two housing treatments; unpredictable housing (which included on different occasions: introduction of an unfamiliar rat; damp bedding; change in light/dark schedule) and predictable housing. After 9 days on the housing treatments, rats were exposed to three untrained (ambiguous) tones of frequencies in between the two trained tones. The rats exposed to the unpredictable housing were slower to press the lever in response to the food tone and the ambiguous tones close to it, than those in the predictable housing. The behaviour of the rats in the unpredictable housing was therefore consistent with a decreased anticipation of positive events.

This first discovery of the existence of a judgement bias in animals has been an important step towards a more direct measure of affective states in animals. The original idea of Harding et al. (2004) has been successfully modified and adapted for several different species and conditions. For example, it has been shown that dogs with separation anxiety express a pessimistic judgement bias (Mendl et al. 2010); rats switched from a high to a low light intensity environment show a more positive bias compared to rats switched from a low to a high intensity light (Burman et al. 2009); depressed rats show a negative bias (Enkel et al. 2010); and starlings displaying stereotypic behaviour show a pessimistic judgement bias (Brilot et al. 2010). Another study by Burman et al. (2008) showed that rats housed in enriched cages (containing paper nesting material, a shelter and nestlets) for 7 weeks and then moved to an unenriched cage showed a more pessimistic judgement bias. Recently, the judgement bias test was modified in our laboratory to make it suitable for use in sheep. Instead of associating a tone with a negative or positive reinforcer, sheep were trained to associate a spatial location with the reinforcers, and used locations in between the positive and negative reinforcers as ambiguous locations. Using this methodology, it was found that the induction of a negative state by administration of a serotonin inhibitor leads to a negative judgement bias (Doyle et al. 2011). Interestingly, short-term stressors such as shearing and release from restraint have both led to a positive judgement bias in sheep (Doyle et al. 2010a; Sanger et al. 2011). Therefore, short-term and long-term stressors may have a different impact on judgement biases.

Little research has been conducted on the effects of positive affective states on judgement biases, and most of this work has focused on environmental enrichment. Brydges et al. (2011) provided some rats with a large cage that contained tubes, boxes and toy houses while other rats were kept in a smaller cage without additional elements. Rats that were kept in the unenriched cage showed a pessimistic bias, while rats that were transferred from the unenriched to the enriched cage expressed a more optimistic bias. Similar results were found in starlings: starlings housed in an enriched cage (with more space, continuous access to water baths, perches and bark) showed a more positive judgement bias compared starlings housed in a standard cage (Matheson et al. 2008).

Assessing judgement biases in animals is therefore a promising method for the measurement of affective states. The judgement bias methodology appears to measure the animals' anticipation of a negative or positive event, and may therefore be a measure of the animals' emotional state. However, more validation work is needed to determine whether the judgement bias is indeed a measure of the animals' affective state and does not result from other factors. This could be done, for example, by comparing the results of judgement bias tests with traditional behavioural and physiological measures. Another alternative is to induce an affective state by means of psychological drugs. It has already been shown that a serotonin inhibitor induces a negative judgement bias in sheep (Doyle et al. 2011), and the effects of other drugs that could potentially induce a positive affect (e.g., opioids, tryptophan or anti-depressants/anxiolytic drugs) could be explored. There are also some practical issues with the methodology. For example, animals learn very quickly that the ambiguous locations remain unreinforced and this limits the number of trials that can be run (Brilot et al. 2010; Doyle et al. 2010b). Therefore, further validation is needed and methodological issues will need to be resolved, but the methodology is promising for use in assessing positive affective states in animals.

Appraisal theory

There is another cognition-based approach to measuring animal's affective states. Appraisal theories have been developed in human psychology and are based on the idea that emotions arise from an individual's evaluation (or appraisal) of a particular situation (Desire et al. 2002; Scherer 2009). Such appraisals are required to assign emotional value to a stimulus so that the individual can give the most appropriate response (e.g., approach, flee, fear, pleasure, etc) to the stimulus (Paul et al. 2005). According to appraisal theory, an individual uses a fixed set of checks to evaluate the significance a stimulus has for them. The outcomes of these checks then determine the emotion that follows from the stimulus. These checks are 1) the novelty of the event (which can be broken down into its suddenness, predictability and familiarity); 2) the intrinsic pleasantness of the event; 3) its goal significance; 4) the implications for the individual's needs and expectations; 5) the possibility of coping with the stimulus; and 6) the compatibility with social or personal standards (Scherer 2001). The checks are hypothesised to be processed in a sequence with a fixed order: the first check is made to determine whether the stimulus requires further attention, the stimulus is then assessed to be of relevance for the individuals needs or goals, and only when the stimulus is found to be relevant will the possibility of coping be triggered (Scherer 2001). This framework of emotional assessment could potentially also be used in animals. It is likely that animals also use a set of checks to determine which stimuli are relevant for them and what the value of such stimuli is. Indeed, there is some evidence that lambs evaluate the relevance of an event by the first check. Desire et al. (2004; 2006) showed that lambs responded to a sudden appearance of a scarf with a startle response and an increased heart rate; and to an unfamiliar object with exploratory behaviour and increased vagal tone. In addition, lambs that could predict the occurrence of a sudden event (by a warning light) showed a weaker startle and cardiac response compared to lambs that could not predict the event (Greiveldinger et al. 2007). Therefore, lambs appear to evaluate the relevance of an event according to its suddenness, predictability and familiarity. Furthermore, it has also been shown that lambs having control over an unpleasant situation (they could interrupt an air blast and a sliding grate preventing access to a food reward by pressing a lever) express less signs of stress than lambs having no control (Greiveldinger et al. 2009). The ability to control a situation therefore also seems to influence the emotional response to an event in animals. The appraisal framework is therefore promising and could be further developed for use in emotional assessment in animals. As with the judgement bias methodology, the appraisal method in animals is a fairly recent development and will need to be further validated. To date, appraisal theory has only been used to assess negative affective states and future studies are expected to extend the research to positive affective states.

Conclusions

Progress is being been made in measuring affective states in animals. Although the focus of research has mostly been on negative affective states, similar methodologies could be used to assess positive affective states. The most promising methodologies for assessing positive affective states are the recently developed judgement bias and appraisal methodologies, although these still need further validation. In the coming years we expect that more studies on positive affect in animals will be conducted and more information will become available on how to induce and assess positive affective states in animals.

References

Amin, N.; Foa, E. B.; Coles, M. E. 1998: Negative interpretation bias in social phobia. *Behaviour Research and Therapy 36(10)*: 945-957.

Apple, J. K.; Minton, J. E.; Parsons. K. M.; Unruh, J. A. 1993: Influence of repeated restraint and isolation stress and electrolyte administration on pituitary-adrenal secretions, electrolytes, and other blood constituents of sheep. *Journal of Animal Science 71(1)*: 71-77.

Ashby, F. G.; Isen, A. M.; Turken, A. U. 1999: A neuropsychological theory of positive affect and its influence on cognition. *Psychological Review 106(3)*: 529-550.

Boissy, A.; Manteuffel, G.; Jensen, M. B.; Moe, R. O.; Spruijt, B.; Keeling, L. J.; Winckler, C.;. Forkman, B. R.; Dimitrov, I.; Langbein, J. et al. 2007: Assessment of positive emotions in animals to improve their welfare. *Physiology & Behavior 92(3)*: 375-397.

Brilot, B. O.; Asher L.; Bateson, M. 2010: Stereotyping starlings are more 'pessimistic'. *Animal Cognition 13(5)*: 721-731.

Broom, D. M. 1991: Assessing welfare and suffering. *Behavioural Processes 25(2-3)*: 117-123.

Brydges, N. M.; Leach, M.; Nicol, K.; Wright, R.; Bateson, M. 2011: Environmental enrichment induces optimistic cognitive bias in rats. *Animal Behaviour 81(1)*: 169-175.

Burgdorf, J.; Panksepp, J. 2001: Tickling induces reward in adolescent rats. *Physiology & Behavior 72(1-2)*: 167-173.

Burman, O. H. P.; Parker, R.; Paul, E. S.; Mendl, M. 2008: A spatial judgement task to determine background emotional state in laboratory rats, *Rattus norvegicus*. *Animal Behaviour 76*: 801-809.

Burman, O. H. P.; Parker, R. M. A.; Paul, E. S.; Mendl, M. T. 2009: Anxiety-induced cognitive bias in non-human animals. *Physiology & Behavior 98(3)*: 345-350.

Dawkins, M. S. 2008: The science of animal suffering. *Ethology 114(10)*: 937-945.

Desire, L., Boissy, A.; Veissier, I. 2002: Emotions in farm animals: a new approach to animal welfare in applied ethology. *Behavioural Processes 60(2)*: 165-180.

Desire, L., Veissier, I.; Despres, G.; Boissy, A. 2004: On the way to assess emotions in animals: Do lambs (*Ovis aries*) evaluate an event through its suddenness, novelty, or unpredictability? *Journal of Comparative Psychology 118(4)*: 363-374.

Desire, L.; Veissier, I.; Despres, G.; Delval, E.; Toporenko, G.; Boissy, A. 2006: Appraisal process in sheep (*Ovis aries*): Interactive effect of suddenness and unfamiliarity on cardiac and behavioral responses. *Journal of Comparative Psychology 120(3)*: 280-287.

Dolan, R. J. 2002: Emotion, cognition, and behavior. *Science 298(5596)*: 1191-1194.

Dolcos, F.; LaBar. K. S.; Cabeza, R. 2004: Dissociable effects of arousal and valence on prefrontal activity indexing emotional evaluation and subsequent memory: an event-related fMRI study. *NeuroImage 23(1)*: 64-74.

Doyle, R. E.; Fisher, A. D.; Hinch, G. N.; Boissy, A.; Lee, C. 2010a: Release from restraint generates a positive judgement bias in sheep. *Applied Animal Behaviour Science 122(1)*: 28-34.

Doyle, R. E.; Hinch, G. N.; Fisher, A. D.; Boissy, A.; Henshall, J. M.; Lee, C. 2011: Administration of serotonin inhibitor p-Chlorophenylalanine induces pessimistic-like judgement bias in sheep. *Psychoneuroendocrinology 36(2)*: 279-288.

Doyle, R. E.; Vidal, S.; Hinch, G. N.; Fisher, A. D.; Boissy, A.; Lee, C. 2010b: The effect of repeated testing on judgement biases in sheep. *Behavioural Processes 83(3)*: 349-352.

Duncan, I. J. H. 2006: The changing concept of animal sentience. *Applied Animal Behaviour Science 100(1-2)*: 11-19.

Enkel, T.; Gholizadeh, D.; von Bohlen und Halbach, O.; Sanchis-Segura, C.; Hurlemann, R.; Spanagel, R.; Gass, P.; Vollmayr, B. 2010: Ambiguous-cue interpretation is biased under stress- and depression-like states in rats. *Neuropsychopharmacology 35(4)*: 1008-1015.

Erhard, H. W.; Mendl, M. 1999: Tonic immobility and emergence time in pigs--more evidence for behavioural strategies. *Applied Animal Behaviour Science 61(3)*: 227-237.

Fraser, D. 2009: Animal behaviour, animal welfare and the scientific study of affect. *Applied Animal Behaviour Science 118(3-4)*: 108-117.

Friston, K. J.; Tononi, G.; Reeke, G. N. Jr., Sporns, O.; Edelman, G. M. 1994: Value-dependent selection in the brain: simulation in a synthetic neural model. *Neuroscience 59(2)*: 229-243.

Gotlib, I. H.; Krasnoperova, E. 1998: Biased information processing as a vulnerability factor for depression. *Behavior Therapy 29(4)*: 603-617.

Greiveldinger, L.; Veissier, I.; Boissy, A. 2007: Emotional experience in sheep: Predictability of a sudden event lowers subsequent emotional responses. *Physiology & Behavior 92(4)*: 675-683.

Greiveldinger, L.; Veissier, I.; Boissy, A. 2009: Behavioural and physiological responses of lambs to controllable vs. uncontrollable aversive events. *Psychoneuroendocrinology 34(6)*: 805-814.

Haaga, D. A. F.; Beck, A. T. 1995: Perspectives on depressive realism: Implications for cognitive theory of depression. *Behaviour Research and Therapy 33(1)*: 41-48.

Harding, E. J.; Paul, E. S.; Mendl, M. 2004: Animal behaviour: cognitive bias and affective state. *Nature 427(6972)*: 312.

Hay, M., Vulin, A.; Génin, S.; Sales, P.; Prunier, A. 2003: Assessment of pain induced by castration in piglets: behavioral and physiological responses over the subsequent 5 days. *Applied Animal Behaviour Science 82(3)*: 201-218.

Held, S. D. E.; Spinka, M. 2011: Animal play and animal welfare. *Animal Behaviour 81(5)*: 891-899.

Hernandez, C. E.; Matthews, L. R.; Oliver, M. H.; Bloomfield, F. H.; Harding, J. E. 2010: Effects of sex, litter size and periconceptional ewe nutrition on offspring behavioural and physiological response to isolation. *Physiology & Behavior 101(5)*: 588-594.

Isen, A. M.; Johnson, M. M.; Mertz, E.; Robinson, G. F. 1985: The influence of positive affect on the unusualness of word associations. *Journal of Personality and Social Psychology 48(6)*: 1413-1426.

Isen, A. M.; Nygren, T. E.; Ashby, F. G. 1988: Influence of positive affect on the subjective utility of gains and losses: it is just not worth the risk. *Journal of Personality and Social Psychology 55(5)*: 710-717.

Jensen, M. B.; Kyhn, R. 2000: Play behaviour in group-housed dairy calves, the effect of space allowance. *Applied Animal Behaviour Science 67(1-2)*: 35-46.

Jensen, M. B.; Vestergaard, K. S.; Krohn, C. C. 1998: Play behaviour in dairy calves kept in pens: the effect of social contact and space allowance. *Applied Animal Behaviour Science 56(2-4)*: 97-108.

Leidig, M. S.; Hertrampf, B.; Failing, K.; Schumann, A.; Reiner, G. 2009: Pain and discomfort in male piglets during surgical castration with and without local anaesthesia as determined by vocalisation and defence behaviour. *Applied Animal Behaviour Science 116(2-4)*: 174-178.

MacLeod, A. K.; Byrne, A. 1996: Anxiety, depression, and the anticipation of future positive and negative experiences. *Journal of Abnormal Psychology 105(2)*: 286-289.

Matheson, S. M.; Asher, L.; Bateson, M. 2008: Larger, enriched cages are associated with 'optimistic' response biases in captive European starlings (*Sturnus vulgaris*). *Applied Animal Behaviour Science 109(2-4)*: 374-383.

Melches, S.; Mellema, S. C.; Doherr, M. G.; Wechsler, B.; Steiner, A. 2007: Castration of lambs: A welfare comparison of different castration techniques in lambs over 10 weeks of age. *The Veterinary Journal 173(3)*: 554-563.

Mellema, S. C.; Doherr, M. G.; Wechsler, B.; Thueer, S.; Steiner, A. 2006: Influence of local anaesthesia on pain and distress induced by two bloodless castration methods in young lambs. *The Veterinary Journal 172(2)*: 274-283.

Mendl, M.; Brooks, J.; Basse, C.; Burman, O.; Paul, E.; Blackwell, E.; Casey, R. 2010: Dogs showing separation-related behaviour exhibit a 'pessimistic' cognitive bias. *Current Biology 20(19)*: R839-R840.

Molony, V.; Kent, J. E.; Robertson, I. S. 1995: Assessment of acute and chronic pain after different methods of castration of calves. *Applied Animal Behaviour Science 46(1-2)*: 33-48.

Mormède, P.; Andanson, S.; Aupérin, B.; Beerda, B.; Guémené, D.; Malmkvist, J.; Manteca, X.; Manteuffel, G.; Prunet, P.; van Reenen, C. G.; Richard, S; Veissier, I. 2007: Exploration of the hypothalamic-pituitary-adrenal function as a tool to evaluate animal welfare. *Physiology & Behavior 92(3)*: 317-339.

Muehlemann, T.; Reefmann, N.; Wechsler, B.; Wolf, M.; Gygax, L. 2011: *In vivo* functional near-infrared spectroscopy measures mood-modulated cerebral responses to a positive emotional stimulus in sheep. *NeuroImage 54(2)*: 1625-1633.

Panksepp, J. 2005: Affective consciousness: Core emotional feelings in animals and humans. *Consciousness and Cognition 14(1)*: 30-80.

Parrott, R. F.; Houpt, K. A.; Misson, B. H. 1988: Modification of the responses of sheep to isolation stress by the use of mirror panels. *Applied Animal Behaviour Science 19(3-4)*: 331-338.

Paul, E. S.; Harding, E. J.; Mendl, M. 2005: Measuring emotional processes in animals: the utility of a cognitive approach. *Neuroscience & Biobehavioral Reviews 29(3)*: 469-491.

Reefmann, N.; Kaszas, F. B.; Wechsler, B.; Gygax, L. 2009a: Ear and tail postures as indicators of emotional valence in sheep. *Applied Animal Behaviour Science 118(3-4)*: 199-207.

Reefmann, N.; Wechsler, B.; Gygax, L. 2009b: Behavioural and physiological assessment of positive and negative emotion in sheep. *Animal Behaviour 78(3)*: 651-659.

Rushen, J. 1991: Problems associated with the interpretation of physiological data in the assessment of animal welfare. *Applied Animal Behaviour Science 28(4)*: 381-386.

Sanger, M. E.; Doyle, R. E.; Hinch, G. N.; Lee, C. 2011: Sheep exhibit a positive judgement bias and stress-induced hyperthermia following shearing. *Applied Animal Behaviour Science 131(3-4)*: 94-103.

Scherer, K. R. 2001: Appraisal considered as a process of multilevel sequential checking. Pp. 92-120 *in*: Appraisal processes in emotion; Theory, Methods, Research, K. R. Scherer, K. R.; A. Schorr, A.; Johnstone, T. *eds*, New York and Oxford, Oxford University Press.

Scherer, K. R. 2009: The dynamic architecture of emotion: Evidence for the component process model. *Cognition & Emotion 23(7)*: 1307-1351.

Sèbe, F.; Duboscq, J.; Aubin, T.; Ligout, S.; Poindron, P. 2010: Early vocal recognition of mother by lambs: contribution of low- and high-frequency vocalizations. *Animal Behaviour 79(5)*: 1055-1066.

Shettleworth, S. J. 1998: Cognition, evolution and behaviour. Oxford, Oxford University Press.

Strunk, D. R; Adler, A. D. 2009: Cognitive biases in three prediction tasks: A test of the cognitive model of depression. *Behaviour Research and Therapy 47(1)*: 34-40.

Vandenheede, M.; Bouissou, M. F. 1993: Sex differences in fear reactions in sheep. *Applied Animal Behaviour Science 37(1)*: 39-55.

Vanderschuren, L. J. M.; Niesink, R. J. M.; Spruijt, B. M.; Van Ree, J. M. 1995: Influence of environmental factors on social play behavior of juvenile rats. *Physiology & Behavior 58(1)*: 119-123.