Review

The emergence of emotional lateralization: Evidence in non-human vertebrates and implications for farm animals

Lisette M.C. Leliveld [a], Jan Langbein [a], Birger Puppe [a,b,∗]

[a] Institute for Behavioural Physiology, Leibniz Institute for Farm Animal Biology (FBN), D-18196 Dummerstorf, Germany
[b] Behavioural Sciences, Faculty of Agricultural and Environmental Sciences, University of Rostock, D-18059 Rostock, Germany

ARTICLE INFO

ABSTRACT

The study and protection of animal welfare are based on the assumption that animals are sentient beings, capable of experiencing emotions. Still, our understanding of animal emotions is limited. In this review we focus on the potential of cerebral-lateralization research to provide new insights into animal emotional processing. Thereby, our aims were, first, to find a universal lateralization pattern in emotional processing across vertebrates and, second, to discuss how knowledge of emotional-lateralization patterns can be used in science and practice to contribute to improve farm-animal welfare. A literature review suggests evidence of lateralized functioning during emotional contexts across the vertebrate classes, from early vertebrates such as fish and amphibians to non-human primates. With the possible exception of fish, all vertebrate classes seem to show a similar lateralization pattern for emotional processing, with a right-hemisphere dominance for processing rather negatively connotated emotions, such as fear and aggression, and a left-hemisphere dominance for processing positively connotated emotions, such as those elicited by a food reward. Thus, both hemispheres are involved in emotional processing and hemispheric dominance may be used as an indicator of emotional valence (negative-positive). Although only a few domestic animal species (e.g. chicken, sheep, dog and horse) have been extensively studied with regard to emotional lateralization, evidence gathered so far suggests that the right-hemisphere dominance for fear and aggression and left-hemisphere dominance in responses to food rewards also applies to these species. Such patterns could be exploited in animal welfare studies to gain insight into how an animal experiences a potentially emotional situation and to improve farm-animal management. Further research should focus on rarely-studied species and on rarely-studied emotional contexts, such as sex and positive social situations, to improve our understanding of animal emotional lateralization.

© 2013 Elsevier B.V. All rights reserved.

Contents

∗ Corresponding author at: Institute for Behavioural Physiology, Leibniz Institute for Farm Animal Biology (FBN), D-18196 Dummerstorf, Germany.
Tel.: +49 38208 68812; fax: +49 38208 68802.
E-mail address: puppe@fbn-dummerstorf.de (B. Puppe).

1. Introduction

Understanding animal emotions is of crucial importance for the improvement of animal welfare. Indeed, the assumption that animals are sentient beings, capable of experiencing emotions, such as fear, frustration and pleasure, lies at the base of animal-welfare science and protection (e.g. European Union, 1997; Mendl and Paul, 2004; Špinka, 2012). Emotions are defined as short-term affective states due to an event (Désiré et al., 2002). Thereby they are distinguished from long-term affective states (moods such as depression), though emotions and moods are inevitably closely connected and influence one another (Mendl et al., 2010). Traditionally the emphasis was on studying 'discrete' or 'basic' emotions (e.g. fear and aggression; Ekman, 1992). However, recently, researchers have argued that emotional states can be represented as locations in two- or three-dimensional space (core affect; Russell, 2003; Mendl et al., 2010), with valence (positive/negative) and arousal (low/high) as relevant emotional dimensions.

The study of emotions is notoriously difficult, especially in non-human animals, since here we miss the most powerful tool: the linguistic self-expression of emotions (Désiré et al., 2002). In animals, assumptions of emotional states are usually derived from behavioural and physiological measurements (e.g. Désiré et al., 2002; Dawkins, 2006). Several researchers have recently argued for a cognitive approach to study emotions in animals (e.g. Mendl and Paul, 2004; Paul et al., 2005). Cognitive approaches facilitate the study of the 'core affect' underlying emotions, enabling better categorization of emotions along the valence and arousal dimensions (e.g. Mendl et al., 2010; Zebunke et al., 2011; Puppe et al., 2012). In addition, approaches such as cognitive appraisal (e.g. Désiré et al., 2002, 2004) and cognitive bias (e.g. Harding et al., 2004) provide new insight into the emotional processing of animals. In this paper we promote the idea that the analysis of cerebral lateralization can be useful as part of a cognitive approach to study animal emotional processing.

Cerebral lateralization refers to hemispheric asymmetries in structure and/or function (Bisazza et al., 1998). Cerebral lateralization was originally considered to be a uniquely human trait (e.g. Warren, 1980). In recent years, however, extensive evidence has been gathered of structural, functional, and behavioural lateralization in many non-human species ranging from fish to non-human primates, indicating ancient evolutionary roots (for reviews see e.g. Bisazza et al., 1998; Rogers, 2002a). Accordingly, all known hemispheric specializations are suggested to have evolved from a basic lateralization pattern, common to all vertebrates, in which the left hemisphere is specialized in the control of well-established patterns of behaviour under ordinary and familiar settings and the right hemisphere specialized in detecting and responding to unexpected stimuli in the environment (MacNeilage et al., 2009). In human research, the experience and processing of emotions are recognized to be lateralized processes, but the precise contribution of each hemisphere to emotional processing in humans is still much debated (for reviews see Davidson, 1995; Demaree et al., 2005). Two major hypotheses on lateralized emotional processing are the 'right-hemisphere hypothesis' and the 'emotional-valence hypothesis' (see Demaree et al., 2005). The 'right-hemisphere hypothesis' suggests that the right hemisphere is dominant in all emotional processing (e.g. Gainotti, 1972; Tucker, 1981). The 'emotional-valence hypothesis' suggests that the right hemisphere is dominant in the processing of negative emotions, while the left hemisphere is dominant in the processing of positive emotions (e.g. Silbermann and Weingartner, 1986). A variation on this latter hypothesis, by Davidson (1995), postulates that approach-related emotional states are processed with a left-hemisphere dominance, whereas withdrawal-related emotional states are processed with a right-hemisphere dominance (termed the 'approach–withdrawal hypothesis'). The above mentioned hypotheses are all supported by experimental evidence (e.g. Wylie and Goodale, 1988; Sobotka et al., 1992; Lee et al., 2004). Although lateralized emotional processing has been studied in non-human animals as well (see Rogers, 2002a), it is still not clear whether there is a universal pattern across species that may correspond to one of the emotional-lateralization hypotheses.

2. Approach

In this paper our first aim is to provide a comprehensive overview of emotional lateralization across vertebrates, in order to discern a universal pattern and find support for one of the emotional-lateralization hypotheses. The overview serves to show how analysis of cerebral lateralization can provide new insights into emotional processing in animals and, consequently, contribute to the improvement of animal welfare. Earlier reviews showed that cerebral lateralization can provide useful insights into other animal-welfare-related topics, such as animal personalities and coping with stress (reviewed by Morgante and Vallortigara, 2009; Rogers, 2010, 2011). We first review the evidence