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Lateralization of behavior in dairy cows in response to conspecifics and novel persons

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ABSTRACT

The right brain hemisphere, connected to the left eye, coordinates fight and flight behaviors in a wide variety of vertebrate species. We investigated whether left eye vision predominates in dairy cows' interactions with other cows and humans, and whether dominance status affects the extent of visual lateralization. Although we found no overall lateralization of eye use to view other cows during interactions, cows that were submissive in an interaction were more likely to use their left eye to view a dominant animal. Both subordinate and older cows were more likely to use their left eye to view other cattle during interactions. Cows that predominantly used their left eye during aggressive interactions were more likely to use their left eye to view a person in unfamiliar clothing in the middle of a track by passing them on the right side. However, a person in familiar clothing was viewed predominantly with the right eye when they passed mainly on the left side. Cows predominantly using their left eyes in cow-to-cow interactions showed more overt responses to restraint in a crush compared with cows who predominantly used their right eyes during interactions (crush scores: left eye users 7.9, right eye users 6.4, standard error of the difference = 0.72). Thus, interactions between 2 cows and between cows and people were visually lateralized, with losing and subordinate cows being more likely to use their left eyes to view winning and dominant cattle and unfamiliar humans.

Key words: dairy cow, dominance, hemispheric processing, visual lateralization

INTRODUCTION

Lateralization occurs when one hemisphere of the brain controls the cognitive processing of a specific situation and it is manifested as a contralateral side

bias, such as handedness (Rogers, 2000; Schönwiesner et al., 2007; Richter et al., 2009). Lateralization is widespread among vertebrates (Basile et al., 2009) and describes those behaviors, including motor, sensory, and cognitive responses, that are consistently biased to one side of the body at either the individual or population level (Baraud et al., 2009; Robins and Phillips, 2010; Komárková and Bartošová, 2013). It is thought that lateralization functions to facilitate multitasking through different tasks being processed in different hemispheres (Güntürkün et al., 2000; Rogers, 2000; Rogers et al., 2004; Dharmaretnam and Rogers, 2005; Ghirlanda et al., 2009) and to aid social communication and predator avoidance (Vallortigara et al., 2010). A better understanding of lateralization in cows may assist in understanding the emotions they experience and what stimuli they perceive to be threatening and stressful.

Ungulates are good candidates for highly lateralized vision, because the extremely lateralized location of their eyes allows them to scan for predators within 2 monocular fields, united in a broad field of vision of approximately 330°, with a blind spot only directly behind them (Piggins and Phillips, 1996). Ruminants orientate toward their object of vision by turning their head rather than their pupils (Piggins and Phillips, 1996). The high degree of decussation of bovine optic nerves in the optic chiasm (Herron et al., 1978) allows sensory cues and information coming from the left visual field to be analyzed in the right cerebral hemisphere and vice versa (Baraud et al., 2009). The right hemisphere is specialized in both perceiving and expressing emotions and serves the function of responding to unexpected stimuli, controlling escape functions, and detecting and responding to predators, especially from the left side (Robins and Phillips, 2010; Rogers, 2010; Komárková and Bartošová 2013). The left eye–right hemisphere specialization for spatial processing in novel or exploratory contexts can be related to broader vigilance functions (Robins and Phillips, 2010). Horses showing preferential left-eye use (indicating dominance

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of the right brain hemispheres) show increased fear and aggression compared with those with dominant left hemispheres (Komárková and Bartošová, 2013). The left hemisphere controls an individual's response to food items and analysis of recalled cues in cattle (Robins and Phillips, 2010), and well-established patterns of behavior performed in nonstressful situations in a wide range of species (Rogers, 2010). Left hemisphere specialization and dominance is most likely in animals not expressing fear or aggression (Komárková and Bartošová, 2013).

Cattle exhibit hierarchical organization within the herd, and the resulting dominance order may reduce aggression and stress within the herd. As stressed animals rely on predominant use of the right hemisphere (Rogers, 2010), lateralization of eye use could be an indicator of stress susceptibility. A link between dominance and another lateralized behavior, persistency of lateralized milking parlor entry, has been found previously (Prelle et al., 2004).

Some animals also display bilateral behavioral asymmetry, with behaviors involving 1 of 2 opposing limbs (e.g., initiation of walking) performed more on either the right or left side of the body, demonstrating a difference in preference or ability between the 2 sides (Annett, 1985). Such laterality may also be expressed by parts of the body extending sideways during routine behaviors; for example, tongue movement when eating. Such behavioral laterality may be related to asymmetry in body morphology. For example, diagonal symmetry of bovine hooves probably derives from asymmetrical walking or lying patterns (Phillips et al., 1996). Lateralized walking in cattle has also been demonstrated as side preferences in a T-maze (Arave et al., 1992), during entry to a milking parlor (Paranhos da Costa and Broom, 2001), and lying (Uhrbrock, 1969; Arave and Walters, 1980; Bao and Giller, 1991). Laterality may also occur because internal body parts are not symmetrical; for example, the fetus is positioned toward the right side of the body, explaining left side laterality during lying in pregnant (Wilson et al., 1999), ruminating (Albright and Arave, 1997) cows.

Cattle prefer to view a novel person in their left eye (Robins and Phillips, 2010), suggesting that they view that person as a potential predator. It is not clear whether similar visual lateralization might be present in cow-to-cow interactions, especially in the case of a subordinate cow engaged in an agonistic encounter with a dominant cow. It is conceivable that a person would be viewed by all cows as a dominant leader of the herd (Albright, 1986), whereas most cows will dominate some of their herdmates. Dominance is in part dependent on temperament (Kramer et al., 2013), and there is increasing evidence that differences in the

degree of lateralization are associated with temperament in a variety of species, such as dogs (Branson and Rogers, 2006; Batt et al., 2009), horses (McGreevy and Thomson, 2006), and humans (DeYoung et al., 2010).

We hypothesized that the social context of cow-cow or cow-people interactions would influence predominant eye use, and that subordinate cows, those in losing encounters, and those showing fearful temperament traits may demonstrate greater use of their left eye than right eye during agonistic encounters with conspecifics and novel encounters with humans, as a result of signal processing in the right hemisphere of the brain. We further anticipated that the response to a human might depend on whether that person appeared familiar or not. In addition, we investigated relationships between eye use laterality and temperament, as well as productivity characteristics that may relate to priority of access to feed resources.

MATERIALS AND METHODS

The study used the dairy herd of the University of Queensland at Gatton, comprising 183 Friesian cows and 50 cows with mixed breed status, based on Friesian crosses with Jersey, Brown Swiss, and Angus. Mean milk yield, BCS (Lowman et al., 1976), and age (\pm SE) of cows in the herd were 25.5 ± 0.47 L/d, 3.2 ± 0.277 , and 4.8 ± 0.13 yr, respectively. At 1700 h, after p.m. milking, cows were turned out into a feedlot, where they were offered a TMR in two 60-m feed bunks (providing 52 cm of trough space per cow), with two 5-m water troughs at one end of the bunks (providing 4.3 cm of trough space per cow), separated by a central concrete passage. At 0500 h, cows were brought in for a.m. milking and afterward, at 0700 h, they were sent out to pasture, from which they returned for p.m. milking at 1445 h.

Study 1: Cow Behavior in the Feedlot and Milking Parlor

All 233 cows, identified from their ear tags, were observed engaging in agonistic interactions at the feed bunk, in the feedlot, and in the field. Preliminary observations determined that most agonistic behavior occurred after milking from 0700 to 0900 h, and from 1130 to 1330 h. All cows were observed by a single recorder (HO) during these times for 25 d, spread over a 5-wk period. During each interaction, each cow was classified as being in 1 of 6 possible positions (Figure 1). To determine the subordinate/dominant status of the cows, 3 subordinate behaviors were recorded, any one of which was assumed to indicate that cows had lost the interaction: *a* = moved body away from other

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