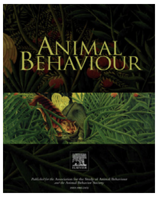
Animal Behaviour 130 (2017) 79–96

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Hens vary their vocal repertoire and structure when anticipating different types of reward

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ARTICLE INFO

Article history:
Received 22 July 2016
Initial acceptance 26 August 2016
Final acceptance 21 April 2017

MS. number: 16-00651R

Keywords:
laying hens
motivation
referential
rewards
vocalizations

The vocalizations of nonhuman animals are considered potential indicators of motivational or internal state. In many species, different call types, and structural variation within call types, encode information about physical characteristics such as age or sex, or about variable traits such as motivation. Domestic chickens, *Gallus gallus*, have an elaborate vocal repertoire, enabling investigation into whether reward-related arousal is encoded within their call type and structure. Twelve hens were given a Pavlovian conditioning paradigm using sound cues to signal the availability of two food rewards (mealworms, normal food), one nonfood reward (a container of substrate suitable for dustbathing), and a sound-neutral event (sound cue, no reward). A muted-neutral treatment (no sound cue, no reward) provided a baseline for vocal behaviour. Sound cues preceded a 15 s anticipation period during which vocalizations were recorded. Hens produced a 'Food call' (previously defined in other studies) in anticipation of all rewards, including the nonfood reward. 'Food calls' and 'Fast clucks' were more prevalent in anticipation of rewards, and most prevalent following the cue signalling the dustbathing substrate, suggesting that this reward induced the most arousal in hens. The peak frequency of 'Food calls' made in anticipation of the dustbathing substrate was significantly lower than those made in anticipation of food rewards, potentially reflecting differences in arousal. Vocalizations that reliably indicate hens' motivational state could be used as measures of welfare in on-farm assessment situations. Our study is the first to reveal variation in the frequency-related parameters of the 'Food call' in different contexts, and to show the prevalence of different call types in reward and nonreward contexts, which may have implications for welfare assessments.

Animal vocalizations contain information encoded within parameters such as frequency (Townsend, Charlton, & Manser, 2014), amplitude (Gustison & Townsend, 2015; Reichard & Anderson, 2015), rate of production (Clay, Smith, & Blumstein, 2012) duration (Dentressangle, Aubin, & Mathevon, 2012) and energy distribution (Linhart, Ratcliffe, Reby, & Špinka, 2015). Some information may be static, relating to age, sex or body size (Briefer & McElligott, 2011; Charlton, Zhihe, & Snyder, 2009). However, variation in these acoustic parameters may also provide 'markers' of internal states (Manteuffel, Puppe, & Schon, 2004; Tallet et al., 2013). Internal states, in this context, refer to states of arousal induced by both internal (e.g. hunger) and external (environmental) stimuli and the interactions between them. Such states exist on a continuum, with arousal levels being in constant flux according to changes in stimuli and internal adjustments to these stimuli (for a detailed discussion see Berridge (2004)).

Flexible traits, such as signaller motivation, can be reflected in vocal frequency, amplitude, duration and rate in both humans (Scherer, 1986) and animals (Briefer, 2012; Taylor & Reby, 2010), as shown in meerkats, *Suricata suricatta* (Hollén & Manser, 2007) and rats, *Rattus norvegicus* (Knutson, Burgdorf, & Panksepp, 2002). The flexible features of vocalizations tend to be subject to certain 'motivation-structural rules' (Morton, 1977). According to this concept, vocalizations produced in one motivational context (e.g. a hostile situation) should vary in structure from vocalizations produced in a very different motivational context (e.g. friendly interactions; Morton, 1977). This theory has been tested in many species including domestic dogs, *Canis lupus familiaris* (Yin & McCowan, 2004), chimpanzees, *Pan troglodytes* (Siebert & Parr, 2003), coatis, *Nasua nasua* (Compton, Clarke, Seidensticker, &

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http://dx.doi.org/10.1016/j.anbehav.2017.05.025

Ingrisano, 2001) and elk, *Cervus canadensis* (Feighny, Williamson, & Clarke, 2006). For most of these animals, the call types commonly produced in hostile contexts are long in duration with a low frequency, whereas in fearful or nonaggressive contexts, short, high-frequency, tonal calls are produced (see review by Briefer, 2012). In addition to different call types, motivation may also be encoded within a sound's structure. For example, the frequency of particular sounds may be lowered when a signaller is feeling aggressive (Bee & Perrill, 1996).

Certain animal vocalizations function referentially, passing information about specific environmental stimuli to receivers (Macedonia & Evans, 1993). To fulfil the criteria for functional reference, calls must be elicited by a narrow range of stimuli, and evoke a response in the receivers as if they had experienced the stimuli themselves (Evans, 1997; Macedonia & Evans, 1993; Marler, Evans, & Hauser, 1992). For example, some species of primate produce different call types according to particular threats or predators (Murphy, Lea, & Zuberbühler, 2013; Zuberbuhler, Noe, & Seyfarth, 1997), which elicit distinctive adaptive responses in the receivers. Functionally referential vocalizations may also encode motivational information at the same time as being referential (Hollén & Manser, 2007). In these instances, the call rate or structural variation within call types may encode information relating to arousal, motivation or urgency (Clay et al., 2012; Manser, 2001). Townsend and Manser (2013) described a motivational-referential continuum, giving the example of meerkats which produce calls that refer to nearby predators and also deliver information about the urgency of the threat. The ‘Food call’ of the chicken, *Gallus gallus* (Collias, 1987; Evans & Marler, 1994), has been described as the most rigorous example of food-specific functional reference within terrestrial animals (Clay et al., 2012). This call appears to meet all the criteria of functional reference; there is acoustic specificity between the stimulus (food) and the signal, and playback elicits feeding-related behaviours in receivers (Clay et al., 2012; Townsend & Manser, 2013). It is also likely that the ‘Food call’ contains motivational information within its acoustic variables.

The anticipation of rewards is thought to increase arousal in animals induced by changes in motivational state, and this, in turn, may elicit vocalizations. Rats, for example, produce ultrasonic vocalizations at 50 kHz in anticipation of rewards such as the presence of a play partner, during tickling from a familiar human or in response to a cue signalling food (Burgdorf & Panksepp, 2006; Knutson, Burgdorf, & Panksepp, 1998; Panksepp & Burgdorf, 2000). By contrast, negative stimuli such as the presence of a predator, or a cue signalling an electric shock, tend to elicit a 22 kHz vocalization in rats (Knutson et al., 2002). This knowledge, theoretically, allows us to assess whether a rat is in a ‘rewarding’ environment, which has implications when determining their welfare. Clear indicators about whether animals are experiencing rewarding or nonrewarding environments may guide decisions made within management systems. The anticipation of rewards induced by signals has been linked to ‘pleasure-based’ (dopaminergic) activity in the brain (Berridge, 1996). Therefore, while stressful environments are known to have deleterious effects on productivity (Broom, 1991), it is reasonable to assume that the reduction of stress through the provision of rewarding environments could positively influence animal health and productivity (Boissy et al., 2007).

The domestic chicken is a good candidate for the study of vocalizations made in anticipation of rewards for three main reasons. First, the behaviour of chickens in anticipation of rewards has already been well documented (Moe, Nordgreen, Janczak, Spruijt, & Bakken, 2013; Moe et al., 2009, 2014; Zimmerman, Buijs, Bolhuis, & Keeling, 2011). Second, behavioural data suggest that the motivational state of chickens changes according to the type of reward (McGrath, Burman, Dwyer, & Phillips, 2016), and therefore it may be possible to link anticipatory behaviour with vocalizations produced in anticipation of rewards. Third, the chicken has a wide and varied vocal repertoire. Between 20 and 25 discrete calls have been documented in various studies (Collias & Joos, 1953; Evans & Evans, 1999; Evans, 1993; Kruijt, 1964; Marx, Leppelt, & Ellendorff, 2001; Woodgush, 1971) including those classed as referential (Evans & Evans, 2007). Interestingly, it seems that motivational information may be encoded within referential calls. Alarm calls, for example, differentiate between terrestrial threats and aerial predators (Evans, Evans, & Marler, 1993) while simultaneously encoding the motivational state of the bird (Kokolakis, Smith, & Evans, 2010).

Chickens have been shown to modify the rate and numbers of their ‘Food calls’ in response to different types of food reward (Marler, Dufty, & Pickert, 1986; Wauters, Richard-Yris, Pierre, Lunel, & Richard, 1999). These changes appear to reflect variation in motivational state according to food type, which indicates there is an opportunity to test for motivational information within a referential call. The ‘Food call’ of chickens is described by various authors as having a characteristic appearance consisting of trains of pulsatile calls delivered in a regular temporal pattern, emphasizing low frequencies, and at a rate of 4–10/s (Collias, 1987; Evans & Marler, 1994). They are given by both males and females, and their structure facilitates location of the sender (Hughes, Hughes, & Covalt-Dunning, 1982). No studies have investigated vocalizations produced by chickens in anticipation of other types of reward, or variation in their acoustic parameters. Therefore, the goal of this study was to characterise vocalizations made in anticipation of different types of reward (different food types known to be ‘rewarding’ to chickens (Bruce, Prescott, & Wathes, 2003), and a substrate suitable for dustbathing). We aimed to investigate whether call parameters varied within the call types according to reward type, and according to whether it was a reward or nonreward. To achieve this, we experimentally induced anticipation of these rewards, using a Pavlovian conditioning paradigm. We tested the hypothesis that chickens would produce specific call types in anticipation of different rewards. We also tested the hypothesis that vocal parameters would differ according to the perceived quality of the reward. These differences would provide information on the motivational state of the signaller, and therefore could be used as indicators of baseline welfare.

METHODS

Subjects and Housing

Twelve ISA Brown hens, approximately 18 weeks old, were obtained from the University of Queensland's poultry unit. The hens were housed in groups of three in pens measuring 266 × 266 cm and 133 cm high. The floor of the home pen was shredded rubber chip, and each pen contained a metal structure used as a perch (149 × 119 cm and 41 cm high) and two nestboxes (40 × 35 cm and 45 cm high). Food (standard layer pellets) and water were available ad libitum in the home pens. The housing had natural as well as artificial light (the latter on between 0600 and 1800 hours). There was no temperature control, but all experimental work was conducted between 0800 and 1230 hours to standardize the conditions. Hens were individually identifiable to the experimenter (N.M.) by plumage colouring, marking and comb size, avoiding the need for individual marking or ringing.

Ethical Note

The methods used in this study were approved by the University of Queensland Animal Ethics Committee (Ref. SVS/314/12). The