



Early vocal recognition of mother by lambs: contribution of low- and high-frequency vocalizations

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In sheep, *Ovis aries*, lambs show a preference for their own mother soon after birth, which is important for their survival. The relative role of low- and high-pitched bleats provided by the mother in this early preference is not clear. While acoustic recognition is clearly established in 2-day-old lambs, it is not known whether lambs use an individual acoustic signature, or some other feature of acoustic communication (type of bleat or a combination of responses) by the mother indicating acceptance. The acoustic analysis of bleats demonstrated that both types of vocalization can support individual discrimination and that frequency spectrum and amplitude modulation exhibit an individual stereotypy. However, the characteristics of bleats and the quantity of encoding information in them differed between low- and high-pitched bleats. In two-choice procedures, we tested the ability of 48 h-old lambs to discriminate between recorded bleats of their own mother and an unfamiliar equivalent mother. Lambs showed a preference for the playback of low-pitched bleats of their own mother, but not for high-pitched bleats. Therefore, 48 h-old lambs can use an individual acoustic signature to recognize their own mother when low-pitched bleats are used. In contrast when high-pitched bleats are used, a vocal exchange between the mother and her lamb appears necessary. We conclude that 48 h-old lambs are able to learn and recognize the individual characteristics of their mother's low-pitched bleats and that this vocal recognition may be important for the establishment of the mother–young bond even at this early stage of the relationship.

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Parental investment is a critical factor of reproductive success in species whose young cannot survive without the help of adults (Trivers 1972). This is, for example, the case in mammals, in which the mother is the only source of food for the newborn and lactation represents a very high energetic expenditure. In such species, preferential maternal care is important to promote investment by the mother in her own progeny, especially in social species (Clutton-Brock 1991). In species that give birth to precocial young (e.g. Bovinae and Caprinae) mutual mother–offspring recognition is generally the rule (Halliday 1983; González-Mariscal & Poindron 2002) and preferential maternal care is ensured by the rapid establishment of a strong exclusive bond with the newborn (Hersher et al. 1963; Lévy et al. 1996; Kendrick et al. 1997). However, even though the mother plays the major role in parental investment, the young animal can also contribute to the success of

mother–offspring recognition by developing a preferential filial relationship with its own mother. Indeed, recognition is crucial to the young animal's survival, whereas an error in recognition represents a smaller cost for adult females. Thus, the selection pressure acting on young animals to recognize their own mothers should be higher than that acting on the mothers to recognize their offspring (Torriani et al. 2006). In precocial neonates, visual and acoustic cues can also help establish a preference for the mother (Nowak 1991; Insley et al. 2003), and this type of young animal therefore offers an excellent opportunity to study the mechanisms by which the neonate develops the preferential relationship that will sustain attachment to its mother. In fact, a critical question in this establishment is whether the neonate learns to recognize some individual physical features of the mother or responds to some signal of acceptance (e.g. licking, allowing access to the maternal udder or production of a particular type of vocalization) or rejection behaviours (e.g. aggression, restlessness or type of vocalization) shown by the mother when interacting with young animals.

The existence of an early preference for the mother is well documented in sheep, *Ovis aries*, which are mostly synchronized, seasonal breeders and, therefore, many young may be born within a very short period of time. Ewes give birth to precocial young

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which are well developed and mobile at birth. Newborn lambs already show some differential heart rate responses to olfactory cues from their mother versus an alien mother (Vince 1993). At 12–24 h old, they also show a behavioural preference for their mother in a double-choice test using visual and acoustic cues (Nowak 1991; Terrazas et al. 1998, 2002), and preference for the mother hidden behind a canvas sheet on the basis only of her vocal cues exists at 48 h of age (Sèbe et al. 2007). Recently, Sèbe et al. (2008) have also demonstrated that mother–young vocal communication and acoustic recognition promote preferential nursing, and therefore vocal communication appears to be a key factor for mother–offspring recognition (see also Searby & Jouventin 2003; Sèbe et al. 2007). Furthermore, during vocal interactions with their 48 h-old lambs, ewes produce two categories of bleats: high pitched and low pitched (Shillito 1972; Poindron & Le Neindre 1980; Dwyer et al. 1998; Dwyer 2008). These two categories of bleat are easily distinguishable by a human ear or by the degree of opening of the mouth: low-pitched bleats are quiet vocalizations produced with the mouth closed whereas high-pitched bleats are loud calls produced with the mouth open. Moreover, it is well established that bleats of ewes differ between individuals and are used for recognition of mothers by lambs several days old (Shillito-Walser et al. 1981; Shillito-Walser & Walters 1987; Searby & Jouventin 2003; Sèbe et al. 2008). However, these studies of an individual vocal signature all deal with high-pitched bleats and were carried out after the first week of parturition. Whether individual differences also exist in maternal low-pitched bleats remains unknown. Dwyer et al. (1998) have suggested that low-pitched vocalizations may be indicative of maternal responsiveness (see also Vince 1986, 1993), as demonstrated in humans (Barratt & Roach 1995). However, the function of these low-frequency vocalizations, or ‘rumbles’, which are produced almost exclusively by the ewe in the presence of her newborn lamb (Shillito 1972), is still poorly understood.

For two main reasons, the possibility that low-pitched bleats may also serve as a basis for the lamb to show a preference for its mother has never been investigated. First, this type of vocalization is frequent only in the early postpartum period (Shillito 1972; Vince 1986; Dwyer et al. 1998; Sèbe et al. 2007). Second, mothers produce mainly high-pitched bleats in the two-choice procedures usually used to test filial preference (Terrazas et al. 2002; Sèbe et al. 2007). None the less, neonates could also use low-pitched bleats and not only high-pitched bleats for individual recognition during the first few days postpartum. Sèbe et al. (2008) have recently demonstrated that, before nursing, vocal communication is important for interindividual recognition. This would be congruent with the fact that early filial preference for the mother depends partly on maternal acoustic cues (Nowak 1991) and that the establishment of this preference is facilitated by the reinforcing action of early suckling activity (Nowak et al. 1997; Goursaud & Nowak 1999; Val-Laillet et al. 2004). As a whole, these results suggest that nursing and postnatal context may be important for vocal learning between lambs and their mothers. Therefore, one possibility to explain the preference shown by 48 h-old lambs for the bleats of their mother is that low- and high-pitched bleats contain a highly individualized vocal signature allowing the lambs to distinguish their own mother from many others; lambs would learn the individual characteristics of their mother's bleats during the initial period of intense interaction with her. The recognition of an individual acoustic signature by lambs has never been demonstrated for low-pitched bleats or for playbacks of high-pitched bleats, and has not been reported before a week of age.

Another possibility to explain the existence of a preference for the vocalizations of the mother before 1 week of age would be that the type of bleat produced by the mother actually guides the lamb

to recognize its mother. The mother may provide an acoustic signal of acceptance, such as a type of bleat or a combination of responses, to attract her lambs. Indeed, in a two-choice situation, a ewe produced mainly low-pitched bleats when her own lamb was close to her in the test, whereas the alien mother kept producing mainly high-pitched bleats (Terrazas et al. 2002). Therefore, when given the choice between two mothers, lambs could go towards their own mother because low-pitched bleats are more attractive to them, as they are the most frequent type of bleat produced by the mother in the first hours of the lamb's life (Vince 1986, 1993; Dwyer et al. 1998; Dwyer & Lawrence 2000).

The aim of the present study was to specify the mechanisms involved in the early acoustic recognition of mothers by their lambs, and to clarify the role of the two categories of bleat, low- and high-pitched, produced by the ewes in the first days postpartum. To investigate this possibility, we carried out experiments 48 h after parturition, when the lambs already show a preference for their mothers and when the ewes produce both low- and high-pitched bleats. We first compared the acoustic parameters of low- and high-pitched bleats for the same mother and calculated the potential of each parameter to encode maternal identity to determine whether both types of bleat could contain the individual signature of the mother. We also compared the encoding potential of the two types of bleat to investigate whether one could be more informative for individual recognition than the other. We then carried out double-choice test experiments to specify the nature of the vocal cues used by 48 h-old lambs to identify their mothers. In our first experiment, we investigated whether low-pitched bleats were more attractive than high-pitched bleats independently of the identity of the female producing them, as suggested by the results of Terrazas et al. (2002) in 24 h-old lambs. This was achieved using a double-choice playback test between low- and high-pitched bleats of an unfamiliar mother. In a second experiment using the same double-choice test design, we investigated the capacity of lambs to show a preference for the bleats of their mothers depending on whether they could interact vocally with them. Lambs were given the choice between the bleats of their own and of an equivalent unfamiliar mother. In one case mothers were hidden behind canvas allowing vocal interaction and access to individual signatures. In the other case the choice was given between two loudspeakers playing back prerecorded bleats thus giving access to vocal signatures only. When testing the preference for played-back bleats, we tested the two types of bleat (low- and high-pitched) separately.

METHODS

Animals

We tested 80 Préalpes-du-Sud lambs at 48 h (± 2 h) postpartum. The experiments were carried out at the INRA Experimental farm of Brouessy, Yvelines, France, where all the lambs were born. Ewes were kept permanently indoors in four communal pens (200 m² each) under intensive management conditions (30 animals/pen). Animals were fed dehydrated lucerne, maize, straw and a supplement of vitamins and minerals according to their physiological needs and had ad libitum access to water. To obtain parturitions concentrated over a few days, reproduction had been fully synchronized by the use of vaginal sponges impregnated with a progestagen to induce ovulation. Lambing was monitored continually during the day and night. When a ewe was about to give birth or just after having given birth, she was penned individually (2 m²) with her young during 6 h postpartum (± 30 min) to mimic the normal period of social isolation occurring at this time (Putu 1990; Lynch et al. 1992). The lambs were ear-tagged, sexed, weighed, and identified with the mother's number sprayed on the

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