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Vocal mother–pup communication in guinea pigs: effects of call familiarity and female reproductive state

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Vocal communication is of special importance in mother–offspring interactions in many precocial mammals, where the offspring are highly mobile. Newborn guinea pigs, *Cavia aperea* f. *porcellus*, make distinct calls when separated from their mother. Assuming that offspring separation calls are important in mother–offspring communication, we predicted guinea pig females would respond more strongly to calls of their own than to calls from unfamiliar pups or other guinea pig calls and would respond to pup calls only during lactation when responses are adaptive. In playback experiments, we tested lactating females' responses to separation calls from their own pups and from unfamiliar pups and to female contact calls. We also tested responses by females in late pregnancy (days 50–60) to separation pup calls. Lactating females responded with significantly more vocalizations to their own and to unfamiliar pup calls than to control sounds. Mothers also responded significantly more strongly to playback of calls from their own pups than to calls from unfamiliar pups, suggesting that mothers are able to use vocal cues in pup recognition. The reproductive state significantly influenced responses: lactating females always responded to pup calls, whereas pregnant females did not respond, suggesting that responsiveness is state dependent.

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Parental care is a defining characteristic of mammals and essential for offspring development and survival. Communication between parent and offspring is important to adjust care to the age and need of offspring. Signals from the young may act to maintain parental responsiveness in the mother (Gonzalez-Mariscal & Rosenblatt 1996) or to indicate a pup's immediate needs, such as for thermoregulation or food, when it becomes separated from its mother, or is in danger of attack by a conspecific or a predator. Thus, the ability to rear offspring successfully can depend fundamentally on the mother's ability to respond appropriately to offspring signals. From a parent's perspective, costly brood care should be expended only on its own offspring (Clutton-Brock 1991). This selects for recognition mechanisms that under most natural circumstances ensure that parental care is restricted to the parent's own offspring (Trillmich 1981; Holmes 1990; Hepper 1991).

In mammals, classic studies on mice, *Mus musculus*, rats, *Rattus norvegicus*, and sheep, *Ovis aries*, showed that olfactory cues are very important in mother–offspring communication (Rosenblatt & Siegel 1975; Porter 1988; Lévy et al. 1996). In rodents, olfactory communication between mother and offspring was shown to be important in animals rearing litters of altricial young in burrows underground (Holmes & Sherman 1982; Schwagmeyer 1988) as well as in precocial species, where newborn offspring are mobile. In precocial guinea pigs, *Cavia aperea* f. *porcellus*, for instance, lactating females olfactorily discriminate their own from unrelated pups (Porter et al. 1973a) and pups recognize their mothers by olfactory cues as well (Jäckel & Trillmich 2003).

Despite the prevalence of olfactory signals in mammals, a number of experimental studies have shown that acoustic communication and recognition can also be important for mother–offspring communication (Shillito & Alexander 1975; Trillmich 1981; Defanis & Jones 1995; Insley 2000; Charrier et al. 2001a). Indeed, particularly in precocial species, selection should favour acoustic recognition to help find and identify the highly mobile offspring in groups of unrelated young (Shillito & Alexander 1975; Insley 2000; Charrier et al. 2001a). Mutual vocal mother–offspring recognition has been well studied in birds (Beecher et al.

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1981a, b; Jouventin et al. 1999; Charrier et al. 2001b), in which the onset of vocal parent–offspring recognition depends largely on when the offspring become mobile and the correlated probability of confounding own with unfamiliar young (Beecher et al. 1981a, b). A similar relation has been found in mammals (Holmes 1990; Hepper 1991). Thus, precocial rodent species, including all caviomorphs, can be expected to use vocal communication and recognition cues in addition to olfactory cues. In these species, mother and offspring actively move around in dense vegetation, where the probability of losing contact and of mixing up young from different litters is much higher than in burrow-living, territorial rodent species, such as ground squirrels (Schwagmeyer 1988; Holmes 1990).

Precocial guinea pigs are excellent for studying acoustic mother–pup communication, since infants follow their mother from the first day and the animals are highly vocal (Porter et al. 1973a, b; Arvola 1974). If mother and pup lose contact, both move around and make specific vocalizations, presumably to re-establish contact (King 1956; Kunkel & Kunkel 1964). If contact is not achieved, pups utter inflected squeaks culminating in the high-intensity wheet (Eisenberg 1974). Such acoustic signals could provide cues of vocal recognition or at least function in alerting parents that have lost their young (Pettijohn 1979). Pup calls arouse females (Berryman 1981), but whether they also cause females to approach or to differentiate between calls of their own and unfamiliar pups is not known.

We carried out three series of playback experiments on female domestic guinea pigs. Since guinea pig pups are highly mobile from birth, we predicted that mothers would respond to playback of pup separation calls by vocalizing and approaching the loudspeaker. If mothers recognize their pups by acoustic cues, we predicted that they would respond more strongly to playback of calls from their own than to calls from unfamiliar pups, or to other guinea pig calls. In contrast, we predicted that pregnant females would not react to pup calls, as responses during pregnancy, when no dependent offspring are present, would seem maladaptive. In experiment 1, we measured responses of lactating females to playback of separation calls from their own pups and responses of a different set of females to playback of calls from unfamiliar pups. We also addressed the same question, i.e. mother–pup recognition, but in a paired design, in which each mother received playback of calls from its own pups and calls from unfamiliar pups. In experiment, 2 we investigated pregnant females' responses to playback of pup separation calls and in experiment 3 we compared lactating females' responses to pup separation calls with their responses to female contact calls.

METHODS

Study Animals

We conducted the experiments in three phases between December 2002 and September 2005 at the Bielefeld University, Germany. We used 44 multiparous and six nulliparous outbred domestic guinea pigs. None of them were used for more than one experiment (i.e. one playback trial with pup calls and a control), except for the within-subject comparison, where we explicitly tested females under two conditions. All subjects were kept indoors on a 14:10 light:dark photoperiod at 20–23°C. Laboratory guinea pig chow (Höveler, Langenfeld, Germany) and water were provided ad libitum, supplemented with hay and fresh food that mainly consisted of carrots. Prior to the experiments we kept all animals in breeding groups of two adult females and one male. Holding compartments measured 0.89 × 0.89 m and 0.50 m high. Until males were removed, female oestrus, defined as the first day when the vagina was fully opened (Touma et al. 2001), was checked daily. The onset of pregnancy was defined as the first day in oestrus.

Playback Stimuli

As stimuli we recorded pup separation calls (experiments 1–3) and female contact calls (experiment 3). Infant guinea pigs usually vocalize intensely when separated from their mother (Pettijohn 1979), uttering low whistles (duration 0.05–150 s; frequency range 0.50–4 kHz) and whistles (duration 0.15–550 s; frequency range 0.50–30 kHz) which frequently occur together in bouts (Berryman 1976). For the separation period, we removed 5–9-day-old pups from their holding compartment and placed them in a recording box (0.30 × 0.25 m and 0.20 m high) in an adjacent room. Pups started to vocalize intensely shortly after separation. In the first experimental phase, we separated pups in pairs to reduce social stress, but used call sequences as playback stimuli when only a single pup was calling ($N = 18$ playbacks). In the second and third experimental phases, we recorded pups that were separated individually ($N = 46$ playbacks). The use of calls recorded from paired pups was balanced across experimental conditions (i.e. playback trials with own pup calls, unfamiliar pup calls and pregnant females). Separation lasted up to 15 min. This duration is within the range of natural feeding intervals, so we did not provide food and water.

To record pup separation calls (Fig. 1a, b) we used a Sennheiser ME 66/K6 directional microphone (0.02–20 kHz ± 1.0 dB) and a Sony TCD-D100 DAT-recorder (0.02–20 kHz ± 1.0 dB) or a Marantz solid state recorder (PMD 670; 0.02–20 kHz ± 0.5 dB). The microphone was located 30 cm above the box. To avoid possible developmental changes in call structure affecting responses or confounding recognition (Charrier et al. 2003), the pup vocalizations that were used as playback stimuli were recorded either on the day of the playback experiment (experiment 1; own pup condition), when the pups were 5–9 days old, from pups of the same age as the pups of the experimental females (experiment 1; unfamiliar pup condition), or from 7–9-day-old pups (experiments 2 and 3). Female contact calls (chuts, experiment 3) were recorded with the same equipment for 10 min. Female contact calls (Fig. 1c) occur in bouts during all social interactions and in general activity, with a duration of 0.025–0.050 s and a frequency range of 0.25–3 kHz (Berryman 1976).

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