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INDIVIDUAL DIFFERENCES IN INFANT GUINEA PIG PUPS ISOLATION WHISTLES

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ABSTRACT

When separated from their mother and other group members, guinea pig *Cavia porcellus* pups emit distinctive high pitched whistles. To determine if these vocalisations are individually distinctive, we recorded the whistles of isolated guinea pig pups, 8 to 10 days old, and subjected their acoustical parameters to discriminant analysis. The results of the reclassification accuracy were higher than random assignment, indicating the existence of individual differences. Individual pup vocalisations did not differ from one another by any single acoustic parameter, but by a set of parameters. Individual recognition of such isolation calls by mothers could play an important role in facilitating reestablishment of contact.

Keywords: distress vocalisation, individual characteristics, pup recognition, guinea-pigs, *Cavia porcellus*.

INTRODUCTION

Individual differences in calls and its use in parent-offspring or mate recognition have been demonstrated in a wide diversity of animals: parrotlets (Wanker et al. 1998), swallows (Beecher et al. 1981), gulls (Charrier et al. 2001), penguins (Jouventin et al 1999), seals (Petrinovich 1974; Renouf 1985), dolphins (Sayigh et al. 1998), bats (Balcombe 1990), domestic pigs (Ilmann et al. 2002), primates (Marler & Hobbett 1975; Lillehei & Snowdon 1978; Snowdon & Cleveland 1980; Smith et al. 1982; Newman & Goedking 1992). In many species, costs of misdirected parental care are high and the mutual parent/offspring recognition of vocalisations has been selected for (Geiss & Schrader 1996; González-Mariscal & Poindron 2002). Infant

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recognition may be especially relevant when infants are mobile and different females with their offspring coexist within a group (Beecher 1991) as occurs in domestic guinea pigs *Cavia porcellus*.

The social group of guinea pigs includes a dominant male, one or more females and their pups and one or more subdominant males (Jacobs 1976; Sachser 1986, 1998). From their very first day of life, pups are mobile, following their mothers and other conspecifics while they forage in grassy environments (King 1956; Rood 1972). Maternal care, in the form of grooming and suckling, is given for about three weeks (Künkele & Trillmich 1997; Künkele 2000). The dominant male, probably the sire of the pups, is tolerant of offspring but does not provide any care (Beisiegel 1993).

There is evidence that both domestic (*C. porcellus*) and wild (*C. aperea*) adult cavies are able to recognise familiar conspecifics (Beauchamp 1973; Beauchamp et al 1979; Ruddy 1980; Martin & Beauchamp 1982; Beauchamp & Wellington 1984; Drickamer & Martan 1992, Cohn et al 2004). Individual recognition, probably of a visual and olfactory kind, plays an important role in the maintenance of mother and pup spatial proximity. Guinea pig pups discriminate their mother from other lactating females (Pettijohn 1979a; Fullerton et al. 1974; Berryman & Fullerton 1976; Niciporciukas et al. 1999, Jackël & Trillmich 2003) and mothers recognise their pups at a close distance (Porter et al. 1973; Tokumaru 2000).

When mothers lose visual and olfactory contact with their pups, proximity may still be regained through the pup's production of isolation or distress vocalisations. Mothers may recognise their pup's isolation calls through individual acoustic features of such vocalisations. Approach responses to playbacks of a combination of pups' vocalisations were observed by Berryman (1981) who did not find any preference of females towards their own pups' playback vocalisations. Berryman (1981) did not, however, contain information about individual differences or signatures in pup calling.

The present study addresses the question of acoustic individuality in the most frequent and specific vocalisation pups emit when separated from their mother and from other members of the group: the isolation whistle. Chut, chutters and whines occur during isolation but are also recorded in other behavioural contexts (Berryman, 1976; Monticelli 2000). The isolation whistle is a distinctive high-pitched whistle, composed of repeated harmonic notes with marked frequency modulation (King 1956; Arvola 1974; Berryman 1976; Pettijohn 1977, 1979b; Coulon 1982; Ades et al. 1994; Hennessy & Richey 1987; Hennessy 1988). Coulon (1973, 1982) reported that separation whistles exert a potent attraction effect over other pups and adult guinea pigs and that they elicit vocal responses ("social cohesion calls") and approach from the mothers.

METHODS

Berryman (1976) distinguished two whistle variants which may be emitted in the same vocalisation bout: low whistles which last 0.05 to 0.15 seconds and contain up to seven harmonics distributed in a frequency band from 0.5 to 4 kHz; and whistles which last 0.15 to 0.55 seconds and contain 3 to 14 harmonics distributed in a frequency band of 0.5 to 30 kHz. We choose here to evaluate individual differences in the high whistles.

Subjects. We studied six 8 day-old guinea pig pups born from four litters of the colony at the Experimental Psychology Department in São Paulo University, descendants of a heterogeneous stock. Each litter was housed with the mother and the father in 90x60x30 cm white polypropylene boxes. Water, rabbit chow and fresh vegetables were offered once a day.

Procedure. Each pup was submitted to three 15-minute isolation sessions, one per day, from the 8^{th} to the 10^{th} day of life. In each session the pup was transported from the colony to the test room, put in a 49x47x27 cm wooden box and left in isolation without auditory contact with other animals. Recordings of the vocalisations emitted were made using a Sennheiser ME88 unidirectional microphone connected to a Sony TCD-D8 DAT recorder (sampling frequency: 48 kHz, frequency response: 20 Hz to 22,000 Hz ± 1.0 dB; dynamic range > 87 dB). The microphone was 50 cm above the box.

Sound analysis. Selected parts of the tape containing whistles were digitised with a 8-bit acquisition card using Avisoft SASLab Pro 3.0 (Raimund Specht, Berlin, Germany). This version generates sonograms with frequencies between 0 and 24 kHz (sampling frequency, 48 kHz). Settings used for the generation of the sonograms were FFT size: 512; bandwidth: 111 Hz; weighting function: Hamming; time resolution: 0.73 ms. Forty-five whistles notes were randomly selected from the 8th to the 10th day of life from each of the 6 pups, totalling 270 notes.

Whistle notes were divided into 3 segments (Figure 1): A, a segment with little or no frequency modulation; B, a segment with marked ascending frequency modulation, and C, a segment with varied frequency modulation, generally a descending one.

The following acoustic parameters were measured: (1) note duration, in seconds; (2) mean intensity of the note [(intensity at the beginning of A + intensity at the beginning of B + intensity at the beginning of C + intensity at the end of C)/4], in dB, (3) frequency modulation of A (difference in Hz between the starting and ending points of the segment), (4) frequency modulation of BC (difference in Hz between the initial point of B and the ending point of C), (5) intensity (dB) and (6) frequency (Hz) of the dominant frequency (frequency with the highest intensity), (7) maximum frequency (last

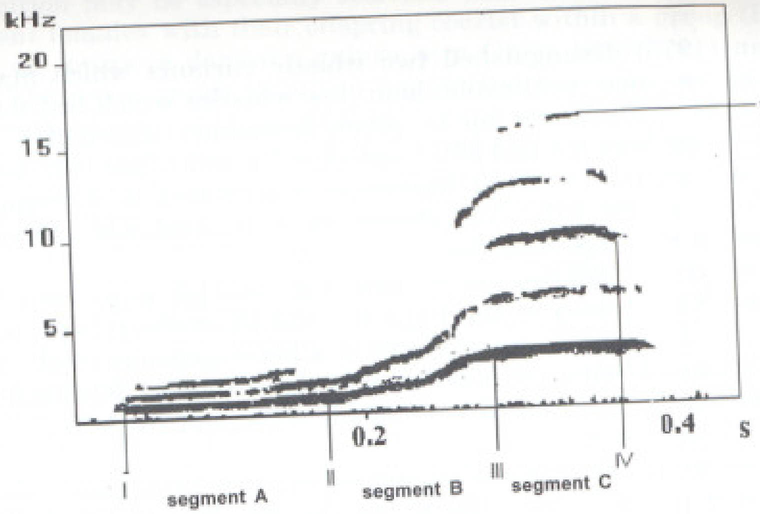

Figure 1: Sonogram of a whistle note. The note is divided into three segments: A, from I to II; B, from II to III; C, from III to IV. The end of the third harmonic (IV) was used as the end of the note. Some acoustic parameters measured were: note duration (from I to IV); maximum frequency (V), mean intensity of the note (average of intensity of fundamental frequency at I, II, III and IV), frequency modulation of fundamental frequency, segment A (frequency at II – frequency at I) and segment B + C (frequency at IV – frequency at II).

harmonic visible in the spectrogram). Except for the maximum and dominant frequencies, all other measures were taken from the fundamental frequency (1st harmonic) (Figure 1).

Statistical analysis. A one-way analysis of variance was performed to test for the significance of differences between individual pups' vocal features (*Statistical Package for Social Science 8.0, SPSS*). A stepwise, cross-validated discriminant analysis was performed to determine the probability of correctly assigning a vocalisation to a specific pup.

RESULTS

Table 1 presents the average values, standard deviations and range of the acoustic parameters measured in each pup vocalisation. Note duration varied from 0.14 to 0.35 seconds and maximum frequency from 6.72 to 21.96 kHz. Dominant frequency occurred, in most notes, in the first harmonic of C (± 2.8 kHz), with mean intensity of -21.04 dB. The marked difference between the minimum and maximum values of the dominant frequency (Table 1) is due to its occurrence either in the first (fundamental frequency) or in the third harmonic of

TABLE 1

Mean values, standard deviation and range of the acoustic parameters measured in whistles notes (45 notes per animal) of six guinea pig pups. Time is expressed in seconds, frequency in kHz and intensity in dB.

Parameters	Pups					
	8a	8b	9a	9c	10	12b
Note duration	0.24±0.04 0.16–0.35	0.21±0.03 0.16–0.33	0.20±0.03 0.15–0.27	0.18±0.03 0.14–0.24	0.20±0.01 0.17–0.23	0.24±0.02 0.19–0.29
Dominant frequency	4.50±2.76 0.86–10.77	2.51±1.73 0.60–9.73	2.63±2.26 0.60–11.63	2.46±3.24 0.60–11.03	2.52±1.65 0.52–10.16	2.21±1.36 0.52–6.12
Maximum frequency	15.60±2.20 10.25–19.98	15.20±4.27 9.56–21.62	13.76±3.39 6.72–20.50	14.90±3.28 9.82–21.71	14.13±3.22 8.27–19.81	14.34±3.49 8.44–21.96
Dominant Intensity	(−14.70)±8.86 (−30.91)–(−0.01)	(−17.00)±6.85 (−29.51)–(−0.02)	(−26.50)±6.37 (−38.76)–(−14.42)	(−15.41)±4.95 (−26.77)–(−1.80)	(−31.74)±5.67 (−38.94)–(11.92)	(−20.89)±7.95 (−38.60)–(−4.71)
Average intensity	(−40.83)±13.47 (−72.37)–(−20.52)	(−46.66)±9.05 (−73.97)–(25.96)	(−55.05)±14.78 (−94.03)–(−33.35)	(−37.50)±4.30 (−46.97)–(−29.20)	(−56.64)±9.98 (−90.48)–(−42.22)	(−47.34)±11.45 (−79.70)–(−28.58)
Frequency modulation of A	0.51±0.16 0.17–0.95	0.36±0.13 0.00–0.60	0.36±0.25 (−0.26)–0.86	0.28±0.10 0.00–0.43	0.30±0.12 0.09–0.60	0.35±0.11 0.17–0.69
Frequency modulation of BC	1.39±0.32 0.43–1.89	1.43±0.25 0.95–1.89	0.41±0.47 (−0.60)–1.29	1.64±0.33 0.95–2.41	1.70±0.46 0.60–2.41	1.58±0.31 0.78–2.24

C. Pup 1, for instance, emitted notes with the dominant frequency located mainly in the third harmonic of C.

Average values correspond approximately to those given by Berryman (1976). The author, however, recorded whistles with a maximum of 30 kHz while the maximum frequency presently obtained was about 22 kHz. This difference is due to differences in the frequency range of the equipment used and is not of major importance to test for individual differences as both fundamental frequency and dominant frequency are under those values.

One-way analysis of variance revealed significant differences between pups in all parameters except maximum frequency: *note duration* ($F_{5,264}$=13.683, p<0.001); *mean note intensity* ($F_{5,264}$=9.477, p<0.001; *A modulation*: $F_{5,264}$=4.325, p<0.001); *BC modulation*: $F_{5,264}$=423.525, p<0.001; *dominant frequency*: $F_{5,264}$=3.994, p<0.01; *dominant frequency intensity*: $F_{5,264}$=18.061, p<0.001; *maximum frequency*: $F_{5,264}$=1.496, p=0.196). The results of *post hoc* analysis showed that significant differences between a given pair of pups are different from those that differentiate any other pair (Table 2). Sonograms of the whistles of two different pups are shown in Figure 2.

Discriminant analysis was performed to estimate individual differences in whistle structure using a multivariate approach (Smith et al. 1982; Newman & Goedeking 1992; Fischer et al. 1995; McCulloch et al. 1999; Ilmann et al. 2002). Table 3 shows the percentage of notes correctly attributed to the sender in the cross-validated discriminant analysis. The sample (n = 270 notes) was randomly divided into two sub-samples. The first column of Table 3 shows the results obtained with one of the samples (analysis sample). The discriminant functions generated with this sample were used to analyse the second one (holdout sample). Results are shown in the second column of Table 3.

All note parameters, except mean intensity, contributed to the differentiation between pups in the cross-validation discriminant

TABLE 2

Significant differences (Bonferroni *post hoc* test, p < 0.05) between individual pups in note duration (1); mean intensity (2); frequency modulation of A (3); frequency modulation of B+C (4); intensity of the dominant frequency (5); dominant frequency (6).

	Pup 12b	Pup 10	Pup 9c	Pup 9a	Pup 8b
Pup 8a	3,5,6	1,2,3,4,5,6	1,3,4,6	1,2,3,4,5,6	1,3,6
Pup 8b	1	2,4,5	1,2	1,2,4,5	
Pup 9a	1,2,4,5	4,5	1,2,4,5		
Pup 9c	1,2,5	1,2,5			
Pup 10	1,2,5				

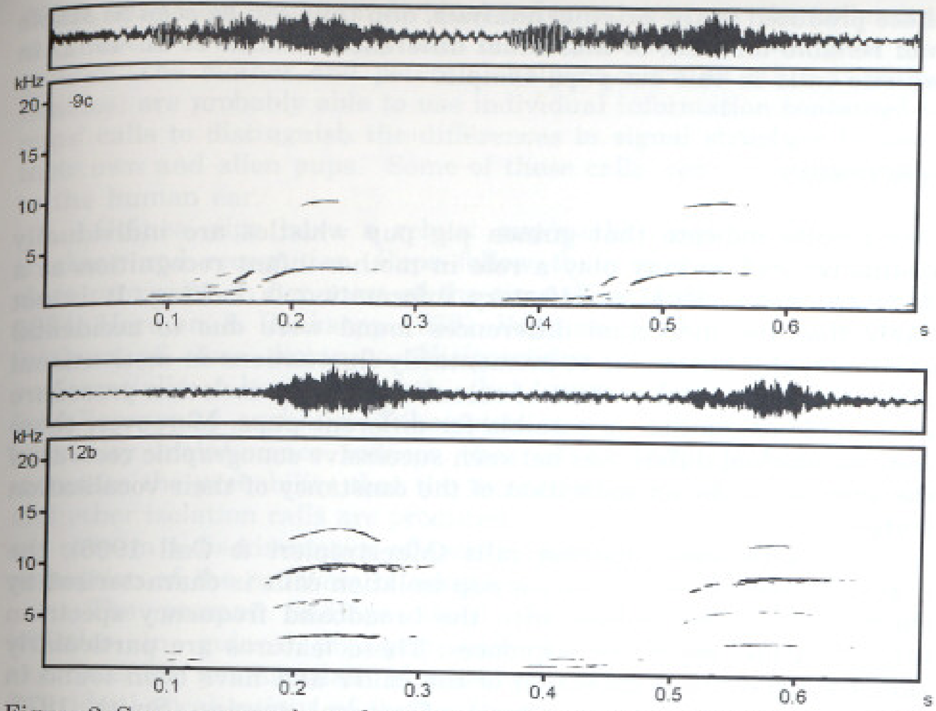

Figure 2: Sonograms and envelope curves of whistle notes of pups 9c and 12b, showing differences in acoustic parameters. Pup 9c: shortest notes (average: 0.18s), energy distributed in all segments, first and third harmonics most intense (darkest colour). Pup 12b: longest note (average: 0.24s), energy concentrated in segment B+C of the third harmonic.

TABLE 3

Percentage of notes correctly attributed to sender in the cross validation discriminant analysis (analysis sample, n=131; holdout sample, n=139)

Pups	Analysis sample	Holdout sample
8a	55.6	48.1
8b	81.0	75.0
9a	78.6	88.2
9c	66.7	58.3
10	61.9	37.5
12b	72.7	78.3
Total	70.2	62.6

analysis. The results of the reclassification accuracy was higher than random assignment (16%; Hair et al. 1995; Geiss & Schrader 1996). The holdout sample produced similar results to the analysis sample indicating that the profiles derived from this data set are the same as those produced in the original analysis, and thus can be seen as stable and reliable markers of individual differences (Smith et al. 1982) in whistle calls in this six pups sample.

DISCUSSION

Our results indicate that guinea pig pup whistles are individually distinctive and so may play a role in mother-infant recognition at a distance, when visual or olfactory information is lacking. It is not likely that the individual differences found were due to accidental environmental factors, or to momentarily fluctuations in motivational state. Environmental context of recording and the isolation procedure were made as similar as possible for different pups. Moreover, there were no marked differences between successive sonographic records of the same animals, an indication of the constancy of their vocalisation features.

As with other distress calls (Maestrepieri & Call 1996), the acoustic structure of guinea pig pup isolation calls is characterised by short, high-pitched pulses, with the broadband frequency spectrum uttered in fast repetitive sequences. These features are particularly suited for accurate localisation of the caller and have been found in the isolation calls of individuals of several species (Smith 1977; Bradbury & Vehrencamp 1998). According to the motivation-structural rules of Morton (1977), such acoustic features indicate that the sender is fearful and will not be hostile if approached or approaching. Stereotypy in general structure is expected in calls emitted under increased predation risk (Newman & Goedeking 1992).

Discriminant analysis and *post hoc* analysis showed that individual pup vocalisations did not differ from one another by any single acoustic parameter, but by a *set* of parameters. The multi-dimensional characteristic of call differences similarly have been reported in grey seal pup vocalisations (McCulloch et al. 1999), in contact calls of pygmy marmosets (Snowdon & Cleveland 1980) and squirrel monkeys (Smith et al. 1982), and in the parental calls of king penguins (Jouventin et al. 1999).

According to Berryman (1976, p. 102), whistles "may serve as proximity-regaining calls, emitted by individuals that are physically separated ... acting as a long-distance auditory indicator of the individual's presence and location". As pups are primarily responsible for the proximity-regaining performance, whistles may have the double function of evoking whistles or other maternal vocalisations and of eliciting in the mother, and possibly other individuals of the group, immobilisation and vigilance behaviour that may facilitate the pups' recovering relevant social contact.

The acoustic features of the whistles, while appropriate for signalling a state of arousal or fear (Eisenberg 1974; Monticelli et al. 2004), may also contain individual information about the caller and may elicit differential approach or alertness responses from the mother. The mother and potential helpers (such as other lactating females) are probably able to use individual information contained in pups' calls to distinguish the differences in signal structure between their own and alien pups. Some of these calls were even discernible to the human ear.

Guinea pigs have a robust pup/mother system of non-vocal tracking and recognition. Pups follow their mother and remain in close proximity to her most of the time (King 1956; Fullerton et al. 1974; Herman & Panksepp 1978). Pups are able to recognise their mothers at close distances (Niciporciukas et al. 1999), and suck preferentially on her, even when other lactating females are available for alloparental suckling (Takamatsu *et. al.* 2003). This system of proximity maintenance reduces the risk of pups getting lost and increases the probability that the mother will be close when whistles and other isolation calls are produced. Recognition could thus depend, not only on a discrimination of *specific features* of whistles, but on the perception of the *nearness* of whistles.

The present findings about the individuality of isolation whistles in guinea pig pups afford the opportunity for an experimental examination of whether mothers actually recognise individual vocalisations of their offspring. Unpublished work on this issue, done in our laboratory, has yielded negative results. Thus it is possible that guinea pig mothers, rely on other information for regaining contact with their own pups even when a vocal signature is available.

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