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Can guinea pig mothers learn to discriminate the whistles of individual pups?

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Abstract: The ability of guinea pig mothers (*Cavia porcellus* Linnaeus, 1758) in discriminating isolation whistles of individual pups was tested. Six mothers were exposed to 24 trials, 12 in which a playback of whistles was followed by the presence of their own pups (CS^+) and 12 in which the whistle's playback was not followed by pups' presentation (CS^-). There were no differences, either in approach behavior or in general activity of mothers between the CS^+ and CS^- trials. An increase in mother's attention was detected in the presence of both playbacks. The lack of discrimination between individual whistles by mothers are discussed in relation to the social organization of guinea pigs, that include high levels of tolerance from adults toward pups and a nonselective attention response to isolation whistles.

Key words: pups recognizement, classical conditioning; guinea pig, *Cavia porcellus.*

Resumo: Mães cobaias podem aprender a discriminar assobios de filhotes individuais? Testou-se a habilidade de mães porquinhos da índia (*Cavia porcellus* Linnaeus, 1958) em discriminar assobios de isolamento de diferentes filhotes. Seis mães passaram por 24 testes. Em 12 deles os filhotes eram apresentados às mães imediatamente após o *playback* do assobio (CS^+). Nos outros testes, o *playback* não era seguido pela apresentação dos filhotes (CS^-). Não houve diferença no comportamento de se aproximar e na atividade geral das mães entre os testes CS^+ e CS^-. Detectou-se aumento na atenção materna na presença de ambos os *playbacks*. A ausência da habilidade materna em discriminar assobios de filhotes diferentes é discutida em relação à organização social dos porquinhos da índia que inclui altos níveis de tolerância aos filhotes por parte dos adultos do grupo e atenção materna não seletiva aos assobios de separação.

Palavras-chave: reconhecimento do filhote, condicionamento clássico, porquinho da índia, *Cavia porcellus*.

Introduction

In many species costs of misdirected parental care are high and a mutual parents/offspring recognition has been selected (González-Mariscal & Poindron, 2002). Individual differences in calls and its use in parent-offspring or mate recognition have been demonstrated in a wide diversity of animals as parrotlets (*Forpus conspicillatus* Lafresnaye, 1848, Wanker *et al*., 1998), swallows (*Riparia riparia* Linnaeus, 1758, Beecher *et al.,* 1981), gulls (*Larus ridibundus* Linnaeus, 1766, Charrier *et al.,* 2001), bats (*Tadarida brasiliensis* I. Geoffroy Saint Hilaire, 1824, Balcombe, 1990), sheep (*Ovis aries* Linnaeus, 1758, Searby & Jouventin, 2003), pigs (*Sus scrofa* Linnaeus, 1758, Ilmann *et al.,* 2001), dolphins (*Tursiops*

truncatus Montagu, 1821, SAYIGH *et al.,* 1998), penguins (*Aptenodytes patagonicus* Miller, 1778, JOUVENTIN *et al*., 1999), seals (*Mirounga angustirostris* Gill, 1866, PETRINOVICH, 1974; *Phoca vitulina* Linnaeus, 1758, RENOUF, 1985), and several species of primates (*Pan troglodytes* Blumenbach, 1775, MARLER & HOBBETT, 1975; *Macaca arctoides* I. Geoffroy Saint-Hilaire, 1831, LILLEHEI & SNOWDON, 1978; *Cebuella pygmaea* Spix, 1823, SNOWDON & CLEVELAND, 1980; *Saimiri sciureus* Linnaeus, 1758, SMITH *et al.*, 1982, *Callithrix jacchus* Linnaeus, 1758, GEISS & SCHRADER, 1996; *Saguinus oedipus* Linnaeus, 1758, MILLER & HAUSER, 2004).

Guinea pig pups, which are precocious and fully mobile at birth, emit high-pitched whistles when out of visual contact with mother during foraging or exploration episodes (KING, 1956; ROOD, 1972). These "separation whistles" are composed of repeated harmonic notes, with a marked frequency modulation (ARVOLA, 1974; BERRYMAN, 1976; COULON, 1973, 1982) and probably have the function of restoring contact with the mother and other members of the group. COULON (1973) reported that separation whistles exert a potent attraction effect on adult guinea pigs and even on other pups and that they elicit vocal responses ("social cohesion calls") and approach from the mothers.

Guinea pig mothers recognize their pups at short ranges, in the absence of vocal cues (PORTER, FULLERTON & BERRYMAN, 1973; TOKUMARU, 2000). Lactating females, although tolerating and suckling alien pups (KING, 1956; ROOD, 1972; FULLERTON *et al.,* 1974; COULON, 1982), give preferential nursing care to their own pups (TAKAMATSU *et al.,* 2003), indicating that they may be sensitive to visual and/or olfactory individual cues. However, relatively little is known about the ability of mothers to recognize pups' vocal calls. BERRYMAN (1981) recorded the approach responses of guinea pig mothers to playbacks of a combination of several pups' vocalizations (whines, chuts, chutters, low whistles and whistles) but did not find any preference for own pups playbacks against alien pups ones.

Lack of discrimination might be attributed, on one hand, to the high similarity and lack of individuality of the calls' pups. On the other hand, lack of discrimination could be interpreted as due to the absence of previous contact of suckling females with the separation whistles of pups (own or alien), not allowing opportunity to learn to discriminate among them. Information about previous acoustic experience of the suckling females is not available in BERRYMAN's paper (1981).

We examined the first hypothesis (lack of acoustic individuality of whistles) in a study in which the acoustic parameters of the isolation whistles of several guinea pig pups were submitted to discriminative analysis. We found that pup whistles were structurally distinctive, at the individual level, differing not by a single, but by a set of parameters (TOKUMARU *et al.,* 2004). Such distinctiveness constitutes an acoustic basis for discrimination of pup's whistles by their mothers.

The present study was conducted to examine the possibility that discrimination might be learned through previous experience with calls. There is empirical evidence in a variety of species that kin recognition depends on contact between the individuals involved, and may develop through repeated exposure to individual features of target individuals. Recognition learning may depend on the building up of an association between call stimuli and the regaining of short-range contact with pups, in a classical conditioning, or Pavlovian way.

Social stimuli have been successfully used as CS+ in the Pavlovian conditioning of approach and species-specific responses (DOMJAN *et al*., 2000). Male gourami fish (*Trichogaster trichopterus* Pallas, 1770) submitted to pairings of a red light with visual access to a female acquired anticipatory approach and courtship responses to the red light (HOLLIS *et al*., 1989); male gerbils (*Meriones unguiculatus*) exposed to a 30-sec presentation of an olfactory stimulus (CS+) that preceded access to a female learned to discriminate it from another one (CS-) not followed by pair mate presentation (VILLAREAL & DOMJAN, 1998). Conditioning may be facilitated when the CS+ includes species-typical cues. Anticipated sexual responses in male quails (*Coturnix japonica* Temminck & Schlegel, 1849) appeared earlier and extinguished later when a female quail head was used as a conditioned stimulus (KRAUSE *et al*., 2003). ADES

et al. (1994) showed that an adult guinea pig learned to distinguish the person who provided food (CS+), from the one who never did (CS-), whistling significantly more in the presence of the CS+.

In this experiment, we used playbacks of pup isolation whistles as CS+ and CS-, in randomly alternating trials. In all trials, pups were first removed from the home cage; in CS+ trials, they were brought back just after playback presentation so that a playback-pups association could be formed; in CS- trials, pups were not presented contiguously with the playback. Isolation from pups is stressful for guinea pig mothers (female guinea pigs, three days postpartum, exhibit increased cortisol levels when separated from pups, Ritchey & Hennessy, 1987): regaining contact should have the reinforcing effect required for conditioning to occur.

Material and Methods

Subjects. Six guinea pigs females (*Cavia porcellus* Linnaeus, 1758), obtained from the Fundação Parque Zoológico de São Paulo, were used in this experiment. They were individually maintained, while pregnant, in white polypropylene cages (90 x 60 x 30 cm) with food and water *ad lib*, at the colony of the Instituto de Psicologia of the Universidade de São Paulo. After the birth of offspring (two to three pups per litter), mother and pups were transferred in their own cage to the experimental room, which was isolated from the colony, and kept at 20°C, under a dark/light cycle of 12:12 h.

Playbacks. Four records of isolation whistles, each from a different seven-day old pup, were used as playbacks. Each pup was isolated for 15 min in a 49 x 47 x 27 cm wooden cage and its vocalizations were continuously recorded with an unidirectional microphone Sennheiser ME88 situated 50 cm above the box and connected to a Sony Dat TCD-D8 recorder (sampling frequency: 48 KHz, frequency response: 20 Hz to 22.000 Hz ± 1.0 dB; dynamic range > 87 dB). 30-sec selections of each of the individual recordings, composed of high whistles, were used as stimuli. A Sony DAT TCD-D8 connected to two loudspeakers Control 1 played playbacks, JBL (frequency response 120-20.000 Hz ± 3.0 dB) placed each at one of the external extremities of the home cage. Playbacks were recorded from pups who were not related or familiar to the mothers in order to eliminate possible bias due to non-controlled past experience with the whistles of such pups.

Procedure. Each female was exposed to two of the whistle recordings, one of them always paired with reintroduction of her own pups (CS+) and the other one that was never paired with reintroduction of pups (CS-). 24 trials, 12 CS+ and 12 CS- trials were randomly scheduled except for the following constraints: the first trial was always a CS+ trial and three consecutive CS+ or CS- was not allowed to occur. Trials were carried out from the 8th to the 14th day of life of the pups, a developmental period in which maternal care occurs predictably (Künkele & Trillmich, 1997; Künkele, 2000). Females received from two to eight trials a day, with a minimum interval of 20 min between successive trials.

Prior to the beginning of a trial, the litter was transferred to a 10 x 10 x 10 cm closed wooden box situated at 1 meter away from the home cage where the mother was to be tested. The trial began when the freezing reactions of the female, induced by the withdrawal of the litter, subsided and when the female resumed relaxed activities, like eating or grooming. This waiting period lasted from 2 to 5 min. From one to two minutes after the beginning of the trial, the 30-sec playback (whether CS+ or CS-) was presented at the cage extremity more distant from the female. In the CS+ condition, all pups were put back into the home box immediately after the end of playback presentation; in the CS- condition, as a control for incidental stimuli, the experimenter simulated, at the end of the playback presentation, the reintroduction of pups, performing the same activities and producing the same sounds as in the other condition. Pups were brought back to the home cage later after a delay of eight to fifteen minutes, out of contiguity with playback presentation. During trials, the experimenter sat quietly behind a black curtain so as to minimize potentially disturbing effects of her presence or movements on the subject's performance.

The behavior of the females was recorded continuously, during trials, with a video camcorder camera placed perpendicularly above the home box. Two periods of each trial were selected for analysis: a 30-sec baseline period prior to the presentation of playback (pre-CS period) and the 30-sec period of playback presentation (CS period). The behavior of females was also observed in the 30 second period which followed CS+ presentation in order to assess the latency and duration of the renewed contact of pups with their mother.

Categories. The duration of the following behavioral categories was obtained from the videotape records of female guinea pigs: *standing still* (standing motionless), *standing with movements* (standing with movements of ears, jaws, head and/or snout or body non-shifting adjustments), *eating or grooming*, *approaching* (getting nearer the source of playback), *withdrawing* (getting farther from the source of playback).

RESULTS

Differences between CS+ and CS- condition. On CS+ trials, when pups where reintroduced to the home box after playback presentation, contact with mother was almost immediate (median latency: 9 sec) and relatively lasting (median time in contact with mother: 14.5 sec). In the CS+ trials there was thus contiguity between playback presentation and the putative reinforcing event (contact with pups), a prerequisite for the acquisition of an association between both events. On CS- trials, females mostly remained still in the period that followed playback presentation.

Discrimination between playbacks was evaluated by comparing the frequency of approaches and withdrawals during the CS period. Approaches to and withdrawals from the source of playbacks occurred only 21 times (out of 144 trials) during the CS period. The females were not more inclined to approach or withdrawal the source in the CS+ condition than in the CS- condition. On CS+ trials, seven approaches to the loudspeaker and eight withdrawals were recorded; on CS- trials, two approaches and four withdrawals were recorded; although there were more approaches and withdrawals in the CS+ condition the difference between the conditions was not significant (Fischer's exact test, $p > 0.05$).

An activity change index (activity score in CS – activity score in pre-CS/activity score in pre-CS) was also used to evaluate discrimination between CS+ and CS-. There was no significant difference between CS+ and CS- behavioral change indexes, either in the first six trials of training [*standing still* (Wilcoxon $Z = -0.104$, $p > 0.05$), *standing with movements* (Wilcoxon $Z = -0.104$, $p > 0.05$), *eating and grooming* (Wilcoxon $Z = -1.213$, $p > 0.05$] or in the six last trials of training [*standing still* (Wilcoxon $Z = -1.362$, $p > 0.05$), *standing with movements* (Wilcoxon $Z = -0.733$, $p > 0.05$), *eating and grooming* (Wilcoxon $Z = -0.524$, $p > 0.05$].

Effect of playbacks on general activity. As there was no significant difference in the duration of the categories between conditions CS+ and CS- or between the first and the last six trials, data were collapsed across conditions and trials for an analysis of the general effect of playbacks. *Standing still* duration was significantly higher in the CS than in the Pre-CS period (Wilcoxon $Z = -2.201$, $p < 0.05$); *eating and grooming* had a significantly lower duration in the CS than in the pre-CS period (Wilcoxon $Z = -2.2$, $p < 0.05$) and *standing with movements* did not differ in duration significantly between pre-CS and CS period (Wilcoxon $p > 0.05$).

DISCUSSION

There was no indication, in the present experiment that guinea pig mothers discriminated between the whistles of two different pups. Whistles playbacks elicited an increase in immobility and a decrease in relaxed forms of performance such as eating and grooming, a result indicative of an increase in level of arousal or attention, but there were no differences in such parameters between CS+ and CS- conditions either at the beginning or at the end of training. It can be inferred that, under experimental conditions such as the present ones at least, guinea pig lactating females neither respond differentially nor learn to discriminate between whistles paired with

reintroduction of pups from whistles not paired with their presence.

The experimental design used seems favorable for the occurrence of learning. Training was carried out during the second week of life, a developmental period marked by increases in pup mobility and by a peak in whistle emission under isolation (Pettijohn, 1979), features which may be propitious for the acquisition of call recognition. The procedure of isolating pups and playing back whistles did not depart markedly from natural conditions: it is comparable to spontaneous calling episodes in which pups get apart from their mother and vocalize. Moreover, care was taken to reduce the stressing aspects of testing: the performance of the females was only recorded when freezing subsided and when relaxed activities were resumed.

CS+ and CS- were acoustically different and both situated in the acoustic range to which guinea pigs auditory system is presumably sensitive. They were thus potentially discriminating. In addition to the approach criterion of evaluating the eliciting effects of playbacks, we used a subtler, possibly more sensitive one, the changes in general activity. None of the criteria indicated any recognition of playbacks.

The discriminating task used here seems to fall into the scope of guinea pigs learning capacity. Guinea pigs, once considered as "notoriously difficult to train" (Dailey *et al.,* 1983), have shown proficiency in several learning tasks related to the one that was here offered to them: vocal conditioning (Burnstein & Wolff, 1967), classical conditioning to auditory stimuli (Galvan & Weinberger, 2002), individual discrimination of urine odors through habituation (Beauchamp & Wellington, 1984), and discrimination of human caretakers (Ades *et al*., 1994).

The fact that guinea pig mothers did not learn to distinguish between two different whistles (together with Berryman's, 1981, negative results) may be taken as an indicative that they normally do not recognize or learn to recognize the whistles of their own pups.

This failure of guinea pig mothers to discriminate between separation calls, even in the context of appropriate learning conditions, is intriguing, as it seems to contradict a plausible adaptationist prediction. Offspring recognition should evolve more in species, such as the domestic cavy, in which breeding occur in relatively dense groups, with a possible overlap of litters, than in more solitary species. Guinea pigs are not the only paradoxical case recorded. Lack of differential reactivity to the vocalizations of own, mobile pups was also reported for a very different species, grey seals, *Halichoerus grypus* Fabricius, 1791 (McCulloch *et al.,* 1999). The authors demonstrated phonographically that *H. grypus* pups have stereotyped and individually distinctive calls. They then performed playback experiments in the field. Mothers did not respond more to the calls of their own pups than to the calls of alien pups. A vocal system of mother-infant recognition could be expected to exist in grey seals once, in this species, pup separation is frequent and alien females eventually injure pups.

Two aspects of the behavior of the guinea pigs may contribute to clarify the no-recognition issue. The first one is *the low social risk of temporary isolation of pups from their mother*. Low risk of social harm for pups apart from their mother may explain why discrimination of vocal individual features was not selected for in guinea pigs.

Guinea pigs social organization is a relatively cohesive one, marked by the existence of multiple social bonding which may be assessed through increases in hormonal levels produced by isolation (Sachser *et al.,* 1998; Hornschuch & Sachser, 2001). Aggressive responses are mainly directed towards strangers (Coulon, 1982) and a notable tolerance of adults in relation to pups prevails. Explicit aggression to pups is rarely observed even when pups are confronted with strange males or virgin or nonlactating females (Berryman & Fullerton, 1976). Our own observations indicate that guinea pig mothers may reject pups (her own or alien ones) when they attempt to suckle, but that driven back pups eventually try again and may finally get attached to the nipple. Lactating females tolerate and suckle alien pups (King, 1956; Fullerton *et al.,* 1974; Rood, 1972; Coulon, 1982; Takamatsu *et al.,* 2003).

The tolerant style of guinea pigs towards immature shows up a tranquilizing nature of contact between an isolated pup and members of his group. Pups isolation whistles cease or decrease, not only in the

presence of the mother, but also in proximity with the father or a strange male and even of siblings (Tokumaru, 1995). Cortisol levels are similarly reduced, in an isolation context, when the mother, other lactating female or siblings are near (Sachser *et al.,* 1998; Hennessy *et al.,* 2000; Graves & Hennessy, 2000; Hennessy *et al.,* 2001).

The second aspect is relative to the *low maternal motivation of guinea pig mothers for searching proximity with pups.* The initiative for searching for contact, in guinea pigs, is an asymmetrical one. Fully mobile at birth, pups recognize their mother (Niciporciukas *et al.,* 1999; Jäckel & Trillmich, 2003) and have most of the responsibility for approaching her when she is still (Seward & Seward, 1940; Porter *et al.,* 1973) or for following her throughout the environment when she is moving (King, 1956; Rood, 1972).

The relatively low motivation of guinea pig mothers to seek contact with pups may be a natural consequence of the pups' mobility and of their persistent following tendency, but it may also result from the species reproductive strategy: guinea pig females, which may become pregnant just after giving birth, might diminish their care giving interest in the present litter as a function of the new investment.

This does not mean that suckling females are indifferent to pups whistles. They obviously react to them, but, as our results show, not selectively. They may answer to isolation whistles with a specific call which guides pups back (Coulon, 1982), and this raises the question of individual recognition by pups of the key vocal characteristics of their mother. The answering vocalization that is also observed in other mammals such as domestic pigs (Ilmann *et al.,* 2001) was recorded just once under our experimental conditions. Suckling females show heightened, non-selective alertness when stimulated with isolation whistles: the immobilization and vigilance they exhibit may favor the return of the pup to the group.

Pups successful tendency for proximity maintenance, in which an olfactory and visual cue presumably play a role, reduces the risk of pups getting lost and increases the probability that the mother will be near when whistles and other isolation calls are produced. Recognition could thus depend, not on a discrimination of *individual features* of whistles, but on the readiness to respond to whistles *in general* and to the perception of the location of the vocalizing pups. Pups normally stay near their mother and nearness by itself may constitute a cue for recognition, a "rule of thumb" for selectively attending to own, but not to alien, pups. Of course, such a system is not perfect, and we would expect the mother to sometimes misdirect parental care.

It is important to note that isolation whistles and pup-mother recognition system, as here described and interpreted, are those of *C. porcellus*, a species which was subjected to domestication for some six thousand years (Kunkel & Kunkel, 1964), and that they are not necessarily identical to those of the wild cavy species, *C. aperea* (Erxleben, 1777). Domestic cavies are, in general, less defensive and less aggressive than their wild counterpart. They habituate more readily to threatening environmental stimuli (including humans), and display a higher frequency of courtship and affiliative behavior (Künzl & Sachser, 1999). Wild cavies, on the other hand, show higher levels of alertness (expressed by behaviors such as rising on hind feet) and defensive behaviors (such as the *drr* call, Berryman, 1976). *C. aperea* pups emit much less whistles when isolated than *C. porcellus* pups, a difference which may indicate a higher sensibility to predation risks (Monticelli, 2000).

Differences such as those may condition the nature and intensity of the mothers' reactions to the isolation calls of pups. Should we expect *C. aperea* mothers, adapted to a less secure environment, to be more acoustically discriminative than *C. porcellus* mothers? Comparative studies with domestic and wild cavies may help clarify this and other functional questions.

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