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Avoiding escalation from play to aggression in adult male rats: The role of ultrasonic calls

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ABSTRACT

Play fighting is most commonly associated with juvenile animals, but in some species, including rats, it can continue into adulthood. Post-pubertal engagement in play fighting is often rougher and has an increased chance of escalation to aggression, making the use of play signals to regulate the encounter more critical. During play, both juvenile and adult rats emit many 50-kHz calls and some of these may function as play facilitating signals. In the present study, unfamiliar adult male rats were introduced in a neutral enclosure and their social interactions were recorded. While all pairs escalated their playful encounters to become rougher, only the pairs in which one member was devocalized escalated to serious biting. A Monte Carlo shuffling technique was used for the analysis of the correlations between the overt playful and aggressive actions performed and the types and frequencies of various 50-kHz calls that were emitted. The analysis revealed that lower frequency (20–30 kHz) calls with a flat component maybe particularly critical for de-escalating encounters and so allowing play to continue. Moreover, coordinating calls reciprocally, with either the same call mimicked in close, temporal association or with complementary calls emitted by participants as they engage in complementary actions (e.g., attacking the nape, being attacked on the nape), appeared to be ways with which calls could be potentially used to avoid escalation to aggression and so sustain playful interactions.

1. Introduction

Play fighting involves partners competing for some advantage, such as biting a particular body area (Aldis, 1975; Symons, 1978). While superficially similar, play fighting can be distinguished from serious fighting by several criteria (Smith, 1997): (1) a resource, such as a piece of food, is not gained or protected; (2) the contact is restrained, or, at least, there are no combat-induced injuries; (3) there are frequent role reversals between a pair, with partners alternating as to which is the attacker and which is the defender; (4) even if chasing ensues following contact, further affiliation is likely; and (5) the presence of play signals. However, play fighting can escalate into serious fighting because either one partner is excessively forceful in its attempts to gain the advantage or, because the recipient fails to recognize that the action performed by the partner is a playful one (Aldis, 1975; Fagen, 1981; Pellis and Pellis, 1998). In these situations in which play fighting can be ambiguous, play signals, such as the primate play face (van Hooff, 1967) and the canid play bow (Bekoff, 1974), can be critical in alleviating the misunderstanding and so maintain the encounters as playful (Palagi et al., 2016b). For example, dogs are more likely to perform play bows before initiating playful bites (Bekoff, 1995), with mutual signaling by the partners leading to more prolonged play bouts (Cordoni et al., 2016).

Although play fighting is most commonly associated with juveniles (Fagen, 1981), in many species it can continue past puberty into adulthood (Pellis, 2002). The play fighting among post-pubertal animals is often used as a means of social assessment and manipulation (Brueggeman, 1978; Palagi, 2011; Pellis and Iwaniuk, 1999, 2000), such as testing their relationships with either peers in established social groups or with strangers to gain or maintain dominance (e.g., Antonacci et al., 2010; Erhlich, 1977; Erhlich and Musicant, 1975; Jones, 1983; Mills, 1990; Newell, 1971). The rougher play typical of post-pubertal play fighting (Fry, 2005; Pellis, 2002) can make such utilitarian use of play both more difficult to distinguish from serious fighting and increase the risk of escalation to serious fighting, raising the importance of play signals in navigating the encounter.

In rats, play fighting is most common in the juvenile period (Meaney and Stewart, 1981; Thor and Holloway, 1984), but continues into adulthood (Pellis and Pellis, 1990, 1991b), when adult males use it as a means of both reinforcing and testing dominance relationships (Pellis and Pellis, 1991a; Pellis et al., 1993). For practical purposes, the play

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fighting of rats can be readily distinguished from serious fighting at all ages. Play involves attack and defense of the nape of the neck which is nuzzled with the snout if contacted (Pellis and Pellis, 1987; Siviy and Panksepp, 1987), whereas serious fighting involves bites directed at the flanks and lower dorsum (Blanchard et al., 1977; Pellis and Pellis, 1987). In addition, serious fighting is associated with a variety of agonistic displays, such as tail rattling, threatening an opponent by such actions as adopting a lateral orientation with an arched body and piloerection, and standing on hind feet from which position the rats vigorously push one another (Barnett, 1975; Grant, 1963). When pairs of adult male rats, either familiar or unfamiliar, encounter one another in a neutral arena, the play can be very rough, with vigorous pushing and defense, and these encounters can involve the performance of agonistic displays, but rarely do they escalate to outright aggressive biting (Pellis and Pellis, 1992; Pellis et al., 1993; Smith et al., 1999; Yamada-Haga, 2002; Kisko et al., 2015b). This suggests that the rats are able to escalate the playful encounter to the brink of aggression, but then signal to one another to enable them to de-escalate, and so maintain it as playful or at least non-injurious.

Except for the possible use of hops (Pellis and Pellis, 1983) and an open mouth facial gesture (Panksepp and Burgdorf, 2003), rats do not have any obvious overtly performed actions that can unambiguously serve as play signals, but they do emit many ultrasonic vocalizations (Burgdorf et al., 2008; Knutson et al., 1998), and some of these may potentially function as play promoting signals (Himmler et al., 2014). These calls are of two types, those around 50-kHz, that are associated with positive affective states such as sex and the administration of psychoactive drugs, and those at 22-kHz, that are associated with negative affective states, such as aggression and drug withdrawal (Brudzynski, 2013; Wöhr and Schwarting, 2013). There remains some ambiguity about whether 22-kHz calls are purely positive and 22-kHz calls exclusively negative. For example, 22-kHz vocalizations are emitted by male rats following ejaculation, suggesting an association with a positive affective state (Bialy et al., 2016); however, once the refractory period is over and the male approaches and mounts the female, the male switches back to emitting 50-kHz calls (Burgdorf et al., 2008). The latter findings suggest a switch from an initial, post-ejaculatory state, when the continued presence of the female may be negative, to one in which her presence is again positively rewarding. Conversely, the usage of 50-kHz calls is not always reflective of a positive state. For example, flat 50-kHz calls can occur in ambiguous situations reflecting at least a partially negative affective state (Wöhr et al., 2017). Thus, there may well be gradations in the usage of 22-kHz and 50-kHz emissions as encounters shift from being positively reinforcing to aversive and back again. This may be particularly evident in cases, such as the one studied in the present paper, in which playful encounters escalate to aggression.

Both 50-kHz and 22-kHz calls have been implicated in mitigating aggression. In the resident-intruder test, an unfamiliar adult male is placed in the home cage of another adult male, and the resident attacks the intruder, directing bites at the lower flanks and dorsum (Blanchard and Blanchard, 1994). In these encounters, the intruders emit 50-kHz calls (Takahashi and Lore, 1983; Thomas et al., 1983), and the likelihood of a biting attack is reduced following the emission of 22-kHz calls by one or both animals (Lehman and Adams, 1977; Lore et al., 1976; Sales, 1972; Sewell, 1967). While the 22-kHz calls are found in a narrow frequency range and have a simple, long, flat profile, the 50-kHz emissions are more variable (Wright et al., 2010). This variability of 50-kHz calls provides the possibility that at least some of these calls may be used for more specific purposes than simply communicating affect (Pellis et al., 2017 (in press); Wöhr et al., 2015).

While some 50-kHz calls have a flat frequency profile, the most commonly emitted 50-kHz calls during play are those that are frequency modulated (FM) (Burgdorf et al., 2008), and of the FM 50-kHz calls, trills are the most common (Himmler et al., 2014; Wright et al., 2010; Burke et al., 2016). While such trilling may reflect the positive affective state induced by play (Panksepp and Burgdorf, 2003), some types of FM 50-kHz calls, though less frequently emitted than trills, are statistically associated with particular actions performed during play, such as when evading contact and when nosing a partner's nape (Himmler et al., 2014; Pellis et al., 2017), suggesting that the animals may be signaling in specific ways to influence the behavior of their partner. Even so, among juveniles, the elimination of the ability to hear (Siviy and Panksepp, 1987) or produce (Kisko et al., 2015a, b) ultrasonic calls has only a modest effect on the frequency and form of play (Kisko et al., 2017). However, in the context of the rougher play present in adult rats, the ability to emit ultrasonic calls appears more critical (Kisko et al., 2015b).

Recently, we showed that the risk of aggression among unfamiliar male rats is greatly elevated when one of the pair has been devocalized (Kisko et al., 2015b). When the rats were introduced into the test arena they investigated one another, and then began to play. The play, which could become increasingly rough, in some cases continued until the rats began to exhibit visual threat signals, and then finally deliver a bite. After a bite, the encounter would gradually become gentler until the animals played again (Kisko et al., 2015b, 2017; Pellis et al., 2017). The pairs with a devocalized member initiated just as much play (i.e., nuzzling attacks to the nape), but also more frequently displayed the various signs of aggression (e.g., tail rattling, piloerection). Most strikingly, while pairs from both groups vigorously pushed one another in the mutual upright position, none of the intact pairs escalated to actual biting, whereas all pairs with a devocalized member did so (Kisko et al., 2015b). These findings suggest that fully vocal pairs may be able to use ultrasonic vocalizations in a manner that can diffuse intense moments of the interaction, such as when they vigorously pushing one another in the mutual upright configuration, from escalating to all-out fighting (Kisko et al., 2017). In the present study, we categorized calls and examined their relationship to specific behaviors on a fine (sub-seconds) time-scale, creating plots of the rate of co-occurrence of each vocalization and behavior. These plots provide insight into how calls are used to coordinate adult social interactions. By comparing vocal usage between pairs of adult rats with and without a devocalized partner, we sought to determine which calls were used in which behavioral contexts to mitigate the risk of a playful encounter escalating to aggression. Presumably, these vocal signals should be present in the intact animals and missing when one partner is devocalized.

2. Methods

2.1. Subjects and experimental procedures

Video and audio files of adult male Long Evans rats encountering one another in dyads in a neutral arena were obtained from our library of data that had been collected in a previous study (Kisko et al., 2015b). The testing and data collecting procedures followed have been detailed elsewhere (Himmler et al., 2013, 2014; Kisko et al., 2015a,b). In brief, 24 85–90 day old rats were used, which had been housed in quads since being weaned at 24 days. Between 28-30 days, two members each from three quads were devocalized by bilateral transections of the recurrent laryngeal nerves following Snoeren and Agmo (2013) and maintained in the same quads until testing. Then, rats unfamiliar with one another were tested in pairs in a 50 cm × 50 cm × 50 cm Plexiglas box, lined with approximately 1–2 cm of bedding for trials lasting 10 min. Each animal was habituated to the testing enclosure for 30 min per day for three consecutive days, then, preceding testing, rats were housed in isolation for 24 h.

For testing, the designated pairmates were placed in the test enclosure and videotaped in the dark using cameras with night shot capability for 12 min (for further procedural details see Himmler et al., 2013). Ultrasonic vocalizations were collected using a high frequency microphone (Model 4939, Brüel & Kjaer, Denmark), with sensitivity to

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