



## Presence of a potential competitor and its individual identity modulate ultrasonic vocalizations in male hamsters



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### ARTICLE INFO

#### Article history:

Received 17 March 2018

Initial acceptance 14 May 2018

Final acceptance 16 July 2018

MS. number: A18-00206R

#### Keywords:

familiarity  
golden hamster  
individual recognition  
sexual ultrasonic vocalization  
social defeat  
Syrian hamster  
USV duration  
USV energy

Animal communication takes place in a complex environment that is constantly modulated by particular social conditions. The majority of examples of signalling behaviours modulated by social context involve the presence of an individual of a particular sex or one that simply represents general competition. However, the identity of the individuals and the social relationships among individuals could also significantly modulate acoustic behaviour. In this study, I examined whether the presence of another male competitor modulates the post-interaction vocal response of a male subject to an oestrous female stimulus in golden hamsters, *Mesocricetus auratus*. I found that the presence of a potential competitor during an interaction with a female across a wire-mesh barrier significantly decreased the duration, tempo and energy of 'post-female calls' over time (experiment 1). Moreover, the call duration and energy of one-note simple calls changed over time depending on the identity of the stimulus male. Males that experienced social conflict and lost a fight maintained call duration and increased the energy of their calls over time, but only if the social interaction with the female was in the presence of another familiar neutral male and not in the presence of a familiar winner male (experiment 2). When the winner male stimulus was present, the duration and energy of the calls produced by the loser decreased with time. Individual recognition between familiar conspecifics with different shared experiences likely modulated the motivational state of the male subject and his vocal response after a social interaction with the female. This study provides new evidence that social complexity (competition and individual recognition) can induce dynamic changes of spectrotemporal features of hamster sexual ultrasonic vocalizations.

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Social environment can exert a strong influence on inter- and intrasexual communication (Bohn, Smarsh, & Smotherman, 2013; Doutrelant, McGregor, & Oliveira, 2001; Searcy & Nowicki, 2005). Animals can vary signals rapidly in response to social conditions and this behavioural plasticity maximizes an individual's fitness (Taborsky & Oliveira, 2012). Competitors influence signalling behaviour in many species. For example, competition can enhance amplitude and duration of electrical signals in fish (Gavassa, Roach, & Stoddard, 2013) or change singing behaviour and territorial song in wrens (Benedict, Rose, & Warning, 2012). On the other hand, a female audience can increase the proportion of highly conspicuous displays used by male Siamese fish to communicate to females and other males (Doutrelant et al., 2001).

The majority of examples of signalling behaviours modulated by context involve the presence of individuals categorized only by sex,

or one that simply represents a general challenge or competition. However, the identity of the individuals and the social relationships built with those individuals involving memories of past experiences could also significantly affect behaviour modulation. Only a few examples have demonstrated such level of social awareness. In zebra finches, *Taeniopygia guttata*, the vocal response of males to their partners' calls and to the calls of familiar females changes depending on the composition of the audience (established mating pairs versus unmated females; Vignal, Mathevon, & Mottin, 2004). Male Siamese fighting fish that lose a fight against another male spend significantly less time displaying towards a female that observed that fight than towards a naïve female that had not (Herb, Biron, & Kidd, 2003). Winner males show no preference in displaying to either female (Herb et al., 2003). Therefore, males' assessments of their own status and females' eavesdropping experiences modify the males' signalling behaviour to reduce the cost of courting females that are less likely to mate with them (Herb et al., 2003).

Although less studied compared to other taxa, rodents commonly exhibit a variety of vocal behaviours. Most rodents produce ultrasonic vocalizations (USVs) during social interactions or

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after encountering scent from conspecifics (Sales, 2010). Intersexual interactions reliably elicit calling behaviour in most rodent species (Barfield, Auerbach, Geyer, & Mcintosh, 1979; Cherry, 1989; Fernández-Vargas & Johnston, 2015; Floody, Pfaff, & Lewis, 1977; Hanson & Hurley, 2012; Kapusta & Sales, 2009; Musolf, Hoffmann, & Penn, 2010; Nyby, 1983; Pierce, Sawrey, & Dewsbury, 1989), but nonsexual and aggressive contexts elicit USVs in some species as well (Chabout et al., 2012; Keesom, Rendon, Demas, & Hurley, 2015; Rieger & Marler, 2018; Wöhr & Schwarting, 2008). However, little is known about whether the presence, number or identity of potential competitors can change and modulate ultrasonic calling behaviour or the acoustic properties of the calls produced during a sexual context. A recent study in mice found that the presence of an anaesthetized male increased the duration and complexity of the USVs produced by a male in response to female odour (Seagraves, Arthur, & Egnor, 2016).

The golden hamster, *Mesocricetus auratus*, is one of many species of rodents that produce USVs during social interactions (Fernández-Vargas & Johnston, 2015; Floody et al., 1977). Males vocalize mainly during and after an interaction with a female (Cherry, 1989; Fernández-Vargas & Johnston, 2015; Floody et al., 1977). In addition to being a species widely used in the study of sexual behaviour, the golden hamster is a model organism for the study of aggression and conditioned defeat (Huhman et al., 2003; Johnston, 2003). Male golden hamsters usually establish a dominant–subordinate relationship during their initial encounter, during which chasing and fighting occur (Huck, Lisk, Allison, & Van Dongen, 1986), and the relationship remains stable over subsequent days (Huhman, Moore, Ferris, Mougey, & Meyerhoff, 1991; Huhman, Moore, Mougey, & Meyerhoff, 1992). Males compete for access to receptive females and females prefer dominant over subordinate males (Huck et al., 1986; Place, Vernon, & Johnston, 2014).

Golden hamsters can also discriminate and recognize previous opponents and adaptively modulate their social response (Bath & Johnston, 2007; Lai & Johnston, 2002; Lai, Ramiro, Yu, & Johnston, 2005; Petrulis, Weidner, & Johnston, 2004). After a series of aggressive encounters, male hamsters that repeatedly lose a fight against the same male, avoid and fear that familiar winner but not familiar neutral males (Lai et al., 2005). This could be considered 'true individual recognition' because the subject is recognizing individuals that are equally familiar but different based on past experiences with those specific individuals (Gabor, Phan, Clipperton-Allen, Kavaliers, & Choleris, 2012; Lai et al., 2005). The ability to recognize and remember specific individuals provides the opportunity to examine how social context play a role in modulating social behaviour and signals such as USVs.

To investigate the possible effects that social context might have in modulating sexual vocal behaviour, I studied 'post-female' USVs produced by males after interacting with an oestrous female across a wire-mesh barrier. The post-female USVs guaranteed the identity of the caller without a doubt. Moreover, post-female USVs are sexually motivated, regulated by gonadal hormones (Fernández-Vargas & Johnston, 2015; Floody et al., 1977; Floody, Walsh, & Flanagan, 1979), and playback of USVs have been found to induce females' approach to the source of ultrasound (Floody & Pfaff, 1977). I examined whether the presence of another male (a potential competitor) modulated the post-female USV response by exposing the male subject to one female, two males or one female and one male. I predicted that males would increase vocal production after interacting with both an oestrous female and another male. In addition, I examined whether the presence and identity of a potential male competitor (e.g. familiar winner) might affect the vocal response of a subordinate male (e.g. loser). Given that loser male hamsters recognize and avoid a familiar winner (Lai et al., 2005), I expected that the presence of a familiar winner would

decrease the vocal production of a loser male after interacting with an oestrous female.

## METHODS

### *Subjects and Animal Housing*

All golden hamsters were laboratory stock derived from Charles River and Harlan Laboratories. They were housed individually after weaning in solid-bottom, polycarbonate cages ( $45 \times 24 \times 20$  cm) with Sani-Chips as bedding, cotton fibre squares as nesting enrichment material and food and water available ad libitum. The colony was maintained in a reversed 14:10 h light:dark cycle. All experiments were performed during the first 6 h of the dark phase of the cycle in a dimly lit room separate from the colony room. All equipment was cleaned with ethanol (50%) to eliminate residual odours after each behavioural trial.

As subject animals, I used hamsters that were randomly assigned to experimental or control groups. As stimulus animals, I used unfamiliar individuals unrelated to the subject. Some subject and stimulus animals had previous experience with odours of other hamsters or prior sexual experience. However, hamsters with prior experiences were distributed evenly among experimental and control conditions. All female stimuli used in this study were tested on the day of oestrus. Golden hamsters have consistent 4-day oestrous cycles, enabling prediction with great accuracy of the day of oestrus (Lisk, 1985). To verify that each subject female was in oestrus, I placed a tester ('nonstudy') male in the female's cage 4 days before testing and confirmed whether the lordosis posture was elicited.

All animal procedures in this study were conducted with approval from the Cornell University Institutional Animal Care and Use Committee (protocol no. 1993-0120).

### *Experiment 1: Effect of Competitors on Male Calling Behaviour*

To examine whether the presence of another potential male competitor can modulate the vocal response of a male subject after interacting with an oestrous female stimulus, I exposed male subjects to one female, two males, or one female and one male and allowed them to interact briefly across a wire-mesh barrier. I used 40 males as subjects (mean  $\pm$  SE: age:  $208.2 \pm 16.5$  days; body mass:  $149.3 \pm 2.6$  g), 27 males as potential competitors (age:  $313.7 \pm 21.4$  days; body mass:  $155.7 \pm 2.7$  g) and 25 oestrous females as stimulus individuals (age:  $217.7 \pm 16.5$  days). There were no significant differences among male subject groups in age (Kruskal–Wallis test:  $\chi^2_2 = 0.02, P = 0.98$ ) or body mass ( $F_{39,2} = 0.25, P = 0.77$ ).

Thirteen males were used twice and one male was used three times as potential competitors but with a different subject each time and with more than 2 days between trials. Similarly, two females were used twice as stimuli. Subject males were randomly assigned to two control groups (Groups 1.1 and 2.1) and one experimental group (Group 1.3) (Fig. 1a). For quick reference, each group can be identified throughout the text by the type of stimulus used specified in parenthesis. Subject males in Group 1.1 (female) ( $N = 13$ ) interacted across the wire mesh only with an oestrous female stimulus. The third compartment was left empty. Subject males in Group 1.2 (two males) ( $N = 13$ ) interacted with two stimulus males. Subject males in Group 1.3 (male, female) ( $N = 14$ ) interacted with an oestrous female and a male. The position of the stimulus hamsters was counterbalanced between left and right to the subject.

### *Social interaction test*

The social interaction took place inside a Plexiglas box ( $91.5 \times 50.5 \times 30.5$  cm) lined with acoustic foam (SONEXone

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