



Who is the boss? Individual recognition memory and social hierarchy formation in crayfish



Nayeli Jiménez-Morales, Karina Mendoza-Ángeles*, Mercedes Porrás-Villalobos, Elizabeth Ibarra-Coronado, Gabriel Roldán-Roldán*, Jesús Hernández-Falcón

Departamento de Fisiología, Facultad de Medicina, Universidad Nacional Autónoma de México, Mexico

ARTICLE INFO

Keywords:

Social learning
Procambarus clarkii
 Agonistic behavior
 Protein synthesis
 Muscarinic receptors
 Memory consolidation

ABSTRACT

Under laboratory conditions, crayfish establish hierarchical orders through agonistic encounters whose outcome defines the dominant one and one, or more, submissive animals. These agonistic encounters are ritualistic, based on threats, pushes, attacks, grabs, and avoidance behaviors that include retreats and escape responses. Agonistic behavior in a triad of unfamiliar, size-matched animals is intense on the first day of social interaction and the intensity fades on daily repetitions. The dominant animal keeps its *status* for long periods, and the submissive ones seem to remember 'who the boss is'. It has been assumed that animals remember and recognize their hierarchical *status* by urine signals, but the putative substance mediating this recognition has not been reported.

The aim of this work was to characterize this hierarchical recognition memory. Triads of unfamiliar crayfish (male animals, size and weight-matched) were faced during standardized agonistic protocols for five consecutive days to analyze memory acquisition dynamics (Experiment 1). In Experiment 2, dominant crayfish were shifted among triads to disclose whether hierarchy depended upon individual recognition memory or recognition of *status*. The maintenance of the hierarchical structure without behavioral reinforcement was assessed by immobilizing the dominant animal during eleven daily agonistic encounters, and considering any shift in the dominance order (Experiment 3). Standard amnesic treatments (anisomycin, scopolamine or cold-anesthesia) were given to all members of the triads immediately after the first interaction session to prevent individual recognition memory consolidation and evaluate its effect on the hierarchical order (Experiment 4).

Acquisition of hierarchical recognition occurs at the first agonistic encounter and agonistic behavior gradually diminishes in the following days; animals keep their hierarchical order despite the inability of the dominant crayfish to attack the submissive ones. Finally, blocking of protein synthesis or muscarinic receptors and cold anesthesia impair memory consolidation. These findings suggest that agonistic encounters induces the acquisition of a robust and lasting social recognition memory in crayfish.

1. Introduction

Agonistic encounters are behavioral displays that include aggression, defense and avoidance, and may result in the establishment of a hierarchical organization. Probably, their primary function is to allow members of a species to regulate their spatial distribution.

They may also regulate access to both food supplies and mates. Agonistic behavior is a fundamental aspect of ecological theories and has been studied intensely in decapods.

Under laboratory conditions, when a triad of unfamiliar crayfish is placed in the same circular aquarium, they interact, displaying their main weapons, the chelipeds, threatening each other. As time passes by, they approach each other until a face-to-face encounter is unavoidable. During the fight, they grab each other, particularly by the appendages

(walking legs). As the encounter escalates, one of the animals in the triad retreats, and the fight continues between the remaining two. One of them will become the dominant and the others the submissive (submissive 1 and submissive 2).

To study decapod agonistic behavior in a quantitative manner, several different strategies and assessment scales have been developed (Bovbjerg, 1953; Christoph, Charlotte, & Huber, 2000; Huber, Daws, Tuttle, & Panksepp, 2001; Huber & Kravitz, 1995) and some mathematical models have been proposed (Hock & Huber, 2006). Bovbjerg proposed to classify agonistic actions in positive and negative contacts. Positive contacts are those performed by a given animal on any other. Negative contacts are those that a given animal receives from any other. The minimum clearly assessed positive contacts are threat, attack and fight. The minimum negative contacts are retreat and avoidance

* Corresponding authors at: Departamento de Fisiología, Facultad de Medicina, UNAM, Apdo. Postal No. 70-250, 04510 Ciudad de México, Mexico (K. Mendoza-Ángeles).
 E-mail addresses: xolotlk@unam.mx (K. Mendoza-Ángeles), roldan26@unam.mx (G. Roldán-Roldán).

responses. The degree of dominance is maximal between the dominant animal and the one that retreated first, and diminishes between the dominant and the defeated one (Bovbjerg, 1953). In dyads of crayfish or lobsters, the pattern is similar but the duration and intensity is quantitatively different (Hernández-Falcon, Basu, Govindasamy, & Kravitz, 2005).

This agonistic behavior has been studied intensely during the last decades and some assumptions have been made, particularly about recognition of conspecifics and memory (Berry & Breithaupt, 2010; Cromarty, Cobb, & Kass-Simon, 1991; Hernández-Falcon et al., 2005; Katoh, Sbragaglia, Aguzzi, & Breithaupt, 2013; Reinhart, Cromarty, Sipala, & Kass-Simon, 2012; Rutishauser, Basu, Cromarty, & Kravitz, 2004). For example, it has been reported that decapod recognition is based on olfactory signals (Karavanich & Atema, 1998b), that do not require training over many repeated trials (Delgado-Morales, Hernandez-Falcon, & Ramon, 2004; Gherardi & Atema, 2005), but rather lobsters show evidence of recognition after a single exposure to a *stimulus* animal (Gherardi & Atema, 2005). Moreover, individual recognition memory appears to last for up to 7 days of isolation without reinforcement (Karavanich & Atema, 1998a) and biogenic amines influence aggressiveness in crayfish but not in the hierarchical order (Huber, Smith, Delago, Isaksson, & Kravitz, 1997; Tricarico & Gherardi, 2007).

During face-to-face interactions, crayfish release urine currents that are propelled by the maxillipeds to each other (Breithaupt & Eger, 2002). It has been proposed that these urine currents contain a putative pheromone responsible for conspecific recognition, since experiments designed to impair urine release or urine detection have shown that the lack of this signal induces an increase in the intensity and duration of agonistic encounters, and hence supporting this hypothesis (Bergman, Martin, & Moore, 2005; Breithaupt, Lindstrom, & Atema, 1999; Delgado-Morales et al., 2004; Denissenko, Lukaschuk, & Breithaupt, 2007). However, since the proposal by Karavanich and Atema (1998) of a putative pheromone released by the contenders, the general idea that during agonistic-aggressive encounters animals recognize each other through this pheromone has gained attention, despite such substance has not yet been isolated.

Visual and mechanical signals are also used during agonistic encounters but they seem to be less important to the outcome (Collen & Dunham, 1987; Delgado-Morales et al., 2004).

We have observed that submissive animals appear to “recognize” the dominant crayfish since the first face-to-face encounter and keep recognizing and avoiding the dominant one for at least 25 days when they are tested on a daily basis (Delgado-Morales et al., 2004). Moreover, it has been proposed that a pair of combatants, that previously established a dominance hierarchy, become unfamiliar after 72 h (Karavanich & Atema, 1998b) or one week (Hernández-Falcon et al., 2005; Karavanich & Atema, 1998a) of full isolation in individual aquaria.

Two mechanisms for social recognition and establishment of hierarchy have been proposed: (1) individual recognition, i.e., the recognition of a phenotypic trait or combination of traits belonging to the opponents (Aquiloni, Gonçalves, Inghilesi, & Gherardi, 2012; Barnard & Burk, 1979; Beecher, 1989; Grier, 1984; Karavanich & Atema, 1998a); and, (2) recognition of *status*, which is defined as the recognition of an unfamiliar combatant's dominance level that has been established during one or several prior encounters (Copp, 1986; Karavanich & Atema, 1998b). However, the response of decapods toward conspecifics is complex and not explained by a single hypothesis (Gherardi, Aquiloni, & Tricarico, 2012; Gherardi & Tiedemann, 2004; Tierney, Andrews, Happer, & White, 2013).

Several questions arise regarding this recognition ability among conspecifics in a hierarchy:

(1) Does it require the formation of an individual memory? (2) How many encounters are needed to fully consolidate this memory? (3) Is it possible to change the hierarchy order by impairing the dominant

animal to behaviorally reinforce its dominance? (4) Is it possible to impair recognition memory consolidation by standard amnesic procedures?

In order to gain insight into these questions, we designed a set of experiments to characterize the individual recognition memory associated with the establishment of a hierarchical order in triads of healthy male crayfish under laboratory conditions. The first experiment was aimed at characterizing the acquisition curve of individual recognition memory. In experiment 2, we analyzed whether the decrease in agonistic activity was due to an individual recognition memory or recognition of *status* through the exchange of the dominant member of each triad in a different triad. In Experiment 3, we attempted to modify the hierarchical order based on this putative recognition memory by completely restricting the dominant animal agonistic behavior. Finally, in the fourth experiment, we tried to impair the establishment of the hierarchical order by blocking the consolidation of this putative recognition memory by standard amnesic procedures.

2. Methods

2.1. Animals

We used young-adult male crayfish *Procambarus clarkii* (Girard, 1852), 20–30 g dry weight, obtained from a local provider. Immediately after their arrival to the laboratory, animals were weighed, fed and placed in individual well aerated aquaria under light-dark cycles of 12 h each (lights-on at 07:00 and lights-off at 19:00). Before the beginning of the experiments, crayfish were isolated for at least one week and starved to increase their aggressiveness (Bovbjerg, 1953). We used only animals in intermoult with complete appendages.

2.2. Agonistic encounters

To avoid biasing the outcome of agonistic interactions, we used triads of crayfish with less than 5% difference in body weight (Scrivener, 1971). Animals were labeled with acrylic enamel.

The arena was a circular plastic aquarium (40 cm diameter) filled with well aerated tap water, 10 cm deep. The recording session lasted for 60 min per trial per day.

Animals were initially separated by a transparent, Y-shaped plastic divider, which allowed visual and chemical communication. After 15 min, the divider was removed and the crayfish could interact for 45 min. They were then returned to their individual aquaria and left there until the next day, when the procedure was repeated. Fights were video-taped and analyzed off-line.

2.3. Acquisition curve

In order to construct the acquisition curve of recognition memory, we repeated the encounters previously described on a daily basis at the same hour for 5 days.

2.4. Effect of exchanging the dominant crayfish among triads

In order to analyze whether the decrease in agonistic activity was due to an individual recognition memory or recognition of *status* we made encounters as described in 2.2 using 8 size-matched triads. After the first encounter, crayfish were returned to their individual aquaria and left there until the next day, when the procedure was repeated but confronting the dominant member of each triad with the submissive 1 and 2 of a different triad (i.e., the dominant was an unknown intruder).

2.5. Modification of hierarchy structure

Previous studies have shown that dominance may be acquired after a single agonistic interaction; however, successive encounters

Download English Version:

<https://daneshyari.com/en/article/7298934>

Download Persian Version:

<https://daneshyari.com/article/7298934>

[Daneshyari.com](https://daneshyari.com)