Physiology & Behavior xxx (2017) xxx–xxx

Contents lists available at ScienceDirect

Physiology & Behavior

journal homepage: www.elsevier.com/locate/phb

Trait aggressiveness does not predict social dominance of rats in the Visible Burrow System

Bauke Buwalda *, Jaap M. Koolhaas, Sietse F. de Boer

Neurobiology, Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands

HIGHLIGHTS

- High offensive aggressivion in a resident-intruder paradigm does not predict social dominance in a mixed-sex colony housing
- Average level of trait aggressiveness of male WTG subjects in a Visible Burrow System is not positively correlated with hierarchical steepness
- In WTG male rats a lower social status not necessarily coincides a maladaptive activation of stress response mechanisms and concomitant stress related behaviors
- Capacity to adopt a behavioral strategy fitting the actual hierarchical ranking position probably defines level of perceived social stress

ARTICLE INFO

Article history:
Received 9 September 2016
Received in revised form 1 December 2016
Accepted 5 January 2017
Available online xxxx

Keywords:
Social rat colony
Hierarchy
Social ranking
Stress of subordination
Rat
Visible Burrow System

ABSTRACT

Hierarchical social status greatly influences health and well-being in mammals, including humans. The social rank of an individual is established during competitive encounters with conspecifics. Intuitively, therefore, social dominance and aggressiveness may seem intimately linked. Yet, whether an aggressive personality trait may predispose individuals to a particular rank in a social colony setting remains largely unclear. Here we tested the hypothesis that high trait aggressiveness in Wildtype Groningen (WTG) rats, as assessed in a classic resident-intruder offensive aggression paradigm predicts social dominance in a mixed-sex colony housing using the Visible Burrow System (VBS). We also hypothesized that hierarchical steepness, as reflected in the number and intensity of the social conflicts, positively correlates with the average level of trait aggressiveness of the male subjects in the VBS.

Clear and stable hierarchical ranking was formed within a few days in VBS colonies as indicated and reflected by a rapid loss of body weight in subordinates which stabilized after 2–3 days. Social conflicts, that occurred mainly during these first few days, also resulted in bite wounds in predominantly subordinate males. Data clearly showed that trait aggressiveness does not predict dominance status. The most aggressive male in a mixed sex group of conspecifics living in a closed VBS environment does not always become the dominant male. In addition, data did not convincingly indicate that in colonies with only highly aggressive males, agonistic interactions were more intense. Number of bite wounds and body weight loss did not positively correlate with trait-aggressiveness of subordinates. In this study, rats from this wild-derived rat strain behave differently from Long-Evans laboratory rats that have been studied up till now in many experiments using the VBS. Strain dependent differences in the capacity to display appropriate social behavior fitting an adaptive strategy to a high or low social ranking position probably play an important role in the level of perceived stress in mixed sex social colonies like the VBS.

1. Introduction

From the very start of his scientific career, Randall Sakai was intrigued by questions on the physiological regulation of mammalian behavior. More specifically, the study of the role of peripheral hormones signaling the bodily state to the brain initiating or altering ingestive behaviors marked his line of research. This interest was sparked during his PhD research in the laboratory of Dr. Alan Epstein at the University of Pennsylvania where he studied the role of aldosterone and angiotensin on salt intake. His subsequent interest in the actions of adrenal steroid hormones on brain and behavior probably were key in joining the lab of Bruce McEwen at Rockefeller University in New York as a postdoc. There he extended his research interest to the actions of glucocorticoids on the hippocampus. This brain region was shown to be have a high density of both glucocorticoid and mineralocorticoid receptors [1] and

* Corresponding author.
E-mail address: b.buwalda@rug.nl (B. Buwalda).

http://dx.doi.org/10.1016/j.physbeh.2017.01.008
0031-9384/

therefore highly sensitive to the modulatory actions of these stress hormones as Robert Sapolsky together with McEwen previously showed [2]. During this postdoc period at Rockefeller University he initiated a collaboration with Bob and Caroline Blanchard from the University of Hawaii (the state where he grew up) and the lab of Bruce McEwen on the behavioral and biological effects of chronic social stress. The Blanchard's had cleverly developed a social housing environment to study rodent social behavior in a more naturalistic setting [3]. In this model, which they called the Visible Burrow System (VBS), male and female rats were housed together in an enclosure where an open arena with an imposed diurnal photoperiod was connected to a continuously dark burrow system consisting of tunnels and small chambers mimicking the underground burrows and nests of rat colonies in the wild. This burrow system was made of transparent Plexiglas material allowing observation of the animals in this part of the cage even though the burrows were kept in continuous dark. This collaboration resulted in a very successful research program supported by numerous grants from both the NSF and the NIH, and it was this line of research on causes and consequences of chronic stress of social subordination that brought us in contact with Randall Sakai.

The neurobiology of social behaviors in rats and mice is a central theme of our research lines that focus on individual differences in offensive aggressive behavior on the one hand and vulnerability to social stress on the other hand. In our social stress research we mainly use the resident-intruder paradigm to study the temporal dynamics of neurobiological, behavioral, and physiological consequences of winning and losing a social conflict in both adult and juvenile rats (for reviews see [4–7]). Since many stress stimuli in humans that lead to psychopathology are of social nature [8], and given the difficulty of studying the pathophysiological processes mediating between psychosocial stress and brain and behavior pathologies in humans, research using animal models with a relatively high face validity such as the consequences of social stress in experimental animal models is highly relevant.

As mentioned above, our laboratory has a long history in studying physiology and behavior of rats and mice in the resident-intruder paradigm of social defeat stress. In this model experimental male animals are introduced into the territory of an experienced aggressive male conspecific. Generally, the intruder is rapidly attacked by the aggressive resident and adopts the classic defensive (avoidance/freezing) and submissive (supine) postures signaling defeat/subjugation. After this social defeat experience, ranging from only one single defeat episode [9,10] to multiple daily defeats [11–13], pronounced changes in (brain)physiology and behavior have been described that may last for weeks or even months [14]. Although principally aimed for adaptation, these changes are frequently linked to neural mechanisms underlying stress related psychopathologies like anxiety, depression and posttraumatic stress disorder (PTSD). Important in this realm is that intruder males are singly housed after the stressful confrontation [15]. To ensure the desired outcome of the social conflict, residents usually have a higher bodyweight, are familiarized with fighting and belong to a strain that express high levels of aggression. In our lab we select residential males from our so-called Wildtype Groningen (WTG) rat strain on the basis of their level of offensive aggressive behavior. These rats are descendants from male and female rat pairs caught in the wild and outbred for many generations under conventional laboratory conditions. There is a large variation in trait-like social behavior amongst these feral rats ranging from animals with very high levels of offensive aggressive behavior to animals that show no or only very little aggressiveness [16]. This individual variation allows selection of male WTG rats with high levels of offensive aggressive behavior for the purpose of defeating experimental animals as intruder males to study acute and lasting consequences of social stress [5–7,12,17]. It also allows a detailed analysis of the neurobiological basis of individual differentiation of aggressive behavior incorporating the regulation of the serotonergic neurotransmitter system and nonapeptides like vasopressin [18] and oxytocin [19] (see for further information [20]).

Chronic stress of psychosocial defeat and subjugation can also be studied by housing defeated animals next to dominant aggressive individuals in the sensory contact model as originally developed by Kudryavtseva [21] in mice and also applied in highly territorial species like the tree shrew [22]. In this experimental approach, one can refer to the stress as psychosocial stress of chronic subordination that can even be better studied in semi-natural rodent colonies.

In the VBS, as developed by the Blanchard lab, it was shown that a social hierarchy is formed rapidly when male and female rats from the Long-Evans strain [23] are housed together in groups. Male subordinates in the VBS are reliably characterized by defensive wound patterns and substantial loss of body weight indicative of social stress. Neuroendocrine changes in the hypothalamic-pituitary-adrenocortical (HPA) and hypothalamic-pituitary-gonadal (HPG) axis, like elevated baseline levels of corticosterone and suppressed testosterone plasma levels supported this interpretation. These neuroendocrine changes coincided with changes in dopaminergic [24] and serotonergic [25] neurotransmitter systems as well as altered hippocampal plasticity and structural morphology [26]. Strikingly, data showed that the subordinate individuals could be divided in two subgroups; a group in which the corticosterone stress response to restraint was heavily suppressed (called non-responsive subordinates (NRS)) and subordinates with a "normal" corticosterone response (stress responsive subordinates (SRS)). Clearly, the NRS rats showed the most profound negative impact of such chronic social subordination stress on their reproductive fitness and overall health [23].

Despite the important consequences of social rank on health and well-being, this individual differentiation in the negative consequences of occupying low social ranking positions in a group has not been explored extensively. It would be very interesting to know whether there are trait-like behavioral characteristics such as general coping style or animal personality that predict the likelihood of an animal to occupy a high or low rank in the social hierarchy that is established in the VBS. Since most animal species, including humans, live within social hierarchical organizations, questions related to causal factors contributing to the acquired ranking position are highly relevant from an evolutionary perspective. There are studies describing behavioral or physiological characteristics of individuals after they reached their hierarchical position characteristics [27,28]. Fewer studies are available, however, linking individual trait characteristics prior to placement in a social hierarchy. In a human study effects of personality and physical attractiveness were related to peer ratings of status [29]. High extraversion predicted a high social status whereas high neuroticism predicted lower status particularly in men. Physical attractiveness predicted higher status only in men.

Since social rank of an individual is mainly established during competitive encounters with conspecifics, intuitively social dominance and aggressiveness may seem intimately linked. Indeed, several older studies in birds [30], fish [31] and primates [32] have demonstrated an association between aggressive behaviors and dominance rank. However, many discrepant studies have also been reported in these same animal species [33–35]. Rank-1 mice in a so-called tube test for dominance were not more aggressive in a resident-intruder test [36] indicating that there is a distinction between aggression and dominance. Hence, although trait-aggressiveness seems likely to contribute to the expression of social dominance, there is also evidence to suggest that these traits may be dissociable.

As mentioned above, we extensively described the neurobiological basis of individual differences in coping styles and offensive aggressive social behavior in the WTG strain. Here, we tested ranking position and behavioral and physiological responses to the VBS in WTG male rats selected for trait-like differences in aggressive behavior. We hypothesized that higher trait aggressiveness would result in an enhanced likelihood to acquire dominance in the VBS social hierarchy. We also hypothesized that hierarchical steepness in colonies, as reflected in the amount of the social conflict-induced body weight reduction and bite

Please cite this article as: B. Buwalda, et al., Trait aggressiveness does not predict social dominance of rats in the Visible Burrow System, Physiol Behav (2017), http://dx.doi.org/10.1016/j.physbeh.2017.01.008