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Growing up in the family or growing up alone influences behavior and hormones, but not arginine vasopressin receptor 1a expression in male African striped mice

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HIGHLIGHTS

- We collected data from males of 16 family groups of striped mice.
- We mimicked alternative reproductive tactics observed in the field in captivity.
- We measured behavior, hormonal and the vasopressin receptor 1a in the brain.
- We found differences in hormone levels and in social behavior, but not in AVPR1a.
- The brains of solitary males are physiologically ready to respond to increased AVP levels.

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ABSTRACT

In many species males display alternative reproductive tactics (ARTs). While males of different tactics differ behaviorally in the field, it is often not known whether these behavioral differences would also occur under standardized laboratory conditions, nor how ARTs are regulated by the brain. In the present study we kept male African striped mice (*Rhabdomys pumilio*) in captivity either in family groups or solitary, to mimic ARTs observed in the field. This allowed us to study these males behaviorally under standardized conditions, to replicate physiological findings from the field, and to study the expression of the arginine vasopressin 1a receptor (AVPR1a) in their brains. Changes in either peptide release or receptor expression (or both) might regulate ARTs with differential timelines, with peptide secretion being faster than receptor expression. As observed in the field, family living males had higher corticosterone but lower testosterone levels than singly housed males. Surprisingly, singly housed males were less aggressive while at the same time having higher testosterone levels. We found no differences in AVPR1a expression. In a previous study it was shown that singly housed males have higher levels of AVP stored in their brain, which potentially could be secreted when the social situation changes, for example to establish social bonds. Our study on AVPR1a suggests the hypothesis that, given that the receptor distribution and expression of singly housed males do not differ from that of family-living males, the brains of singly-housed males have a similar capacity to be responsive to AVP when given the chance to interact socially.

1. Introduction

In many species, males display alternative reproductive tactics (ARTs) to optimize their individual reproductive success [1]. In some species these tactics are genetically determined and fixed for life. In other species with plastic tactics males can change from one tactic to another depending on their own condition (age, body mass) and on environmental conditions [1,2]. However, from a proximate point of view it is not well understood which behavioral, hormonal and neuroendocrine changes are associated with tactic changes.

In species with plastic ARTs, it is difficult to distinguish how far the behavioral differences between tactics represent internal motivational difference between males, or are simply triggered by differences in environmental stimuli. An example of externally induced behavioral differences would be if males of the dominant tactic (also called bourgeois tactic) might be more aggressive because they are typically larger

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than the other males they encounter, while sneaker males might be less aggressive only because their opponents are larger than themselves. It is important to test males of different tactics under standardized conditions; for example, always with an opponent male that is smaller than the focal male.

It is well known that males following differing ARTs may differ in their hormonal profiles. Dominant males typically have higher androgen levels [2,3] and lower glucocorticoid levels [2]. In contrast to steroids, we know very little about the role of neuropeptides in the regulation of ARTs. The neuropeptide arginine vasopressin (AVP) modulates social behaviors by activating its receptor 1a (AVPR1a) [4,5]. Variation in this receptor has been shown in brain areas of the "social behavior network" (lateral septum, amygdala, ventral pallidum) [6] which are known to regulate social recognition and pair bond formation [7,8]. Experimentally induced expression of AVPR1a in laboratory mice increased pro-social behaviors [5]. It has been suggested that variation in the expression of AVPR1a explains a significant amount of variation in social behavior of voles of the genus *Microtus*, both within [4,9] and between species [10]. While there is good evidence for an important role of AVPR1a in the regulation of social behavior in laboratory rodents, little is known about its role in the regulation of ARTs, with the exception of one field study showing differences in AVPR1a expression in brain areas involved in spatial memory between territorial males and wanderers of the prairie vole (*Microtus ochrogaster*) [9] but not in brain areas suggested to be important for pair-bonding in prairie voles [32,33]. ARTs are typically studied in the field and not in the laboratory. To study AVPR1a expression one has to sacrifice the animals and collect the brains, which is typically not an option in field studies, as this would greatly affect the entire study population. Therefore, it is important to be able to study ARTs in captivity, where such samples can be collected.

One species with male ARTs that can be studied both in the field and in captivity is the African striped mouse (*Rhabdomys pumilio*). Male striped mice have three alternative reproductive tactics that differ in their hormone levels [11] and in reproductive success [12]: 1. Philopatric males remain in their family group after reaching adulthood. They have very low reproductive success (with neighboring females), low testosterone and high corticosterone levels. Philopatric males typically switch to another tactic when they become heavier. 2. Solitary roamers leave their family group and live alone. They have very high testosterone and low corticosterone levels and typically low reproductive success. They might later immigrate into a group of communally breeding females and become 3. territorial breeding males with somewhat lower testosterone levels, low corticosterone levels and high reproductive success. Males can switch between tactics [11] and their hormonal profiles change as they do so [13]. If population density is very high, most males remain as adult philopatrics in their family group, but when population density is very low, many males become solitary roamers when reaching puberty [14]. Thus, within the same species and same population, males might either grow up in extended family groups or become solitary, representing two very different social pathways.

These tactics as observed in the field have been mimicked in captivity by separating brothers at an age of 3 weeks [14]. One brother remained in the family, representing the philopatric tactic, while his brother was housed singly, representing the roaming tactic. This leads to predicted physiological differences, with singly housed males showing lower corticosterone and higher testosterone levels, becoming sexually mature at an earlier age, developing larger testes and producing more sperm [15–17]. In the present study we used the same experimental approach and we had three aims. (I) We compared the social behavior of family *versus* singly housed males, to determine whether males following simulated ARTs differ in social behavior when tested under identical standardized conditions. We predicted that family housed males would show more aggression towards strange males, because families defend territories while roamers do not [11,18,19]. We further predicted that singly housed males would show more pro-social behaviors towards strange females than family-housed males, as roamers would be more ready to mate. (II) We measured steroid hormone levels and predicted singly house males to have higher testosterone and lower corticosterone levels than their family housed brothers. (III) We measured AVPR1a in the brains of males using all three tactics to examine whether differences in AVPR1a expression are associated with different housing conditions (social *versus* solitary).

2. Materials and methods

2.1. Animals

The colony consisted of animals originally trapped in 2002 in the Succulent Karoo (Goegap Nature Reserve) in South Africa. Animals were bred at the research station in Goegap under natural weather conditions and F10 descendants were exported from there to the University of Zurich in October 2006 where breeding continued. Animal ethical clearance for the experiments was provided by the Kantonale Veterinärmt of the Kanton Zürich in Switzerland (ethical clearance number 91/2006).

2.2. Housing conditions

The study took place from November 2006 to June 2007. Animals were housed at the University of Zurich under an 11.5:12.5 h light regime. Wild rodents kept in captivity are prone to develop stereotypic behavior (for striped mice see [20]) which is known to both affect social behavior as well as physiology and brain structure [21]. Thus, all animals were housed under super-enriched conditions which were successful in avoiding the development of stereotypic behavior (recorded during 15 min observations per individual): none of the 16 family housed males and none of the 16 singly housed males showed any stereotypic behaviors. Wheel running was observed in 6 family-housed and in 4 singly-housed males and did not differ between the two treatments (82.7 ± 146.3 s *vs.* 55.8 ± 116.6 s respectively; $T = 9$, $W = 18$, Wilcoxon-test; $p = 0.25$).

Pairs and families were housed in two 50 × 30 × 30 cm glass tanks which were connected to one another by a flexible plastic tube. A second tube was connected to one 20 × 13 × 15 cm plastic cage (type 4 cage) which contained a water bottle. Single individuals were housed in one glass tank connected to two plastic cages. All tanks and cages had 5 cm of wood shavings as bedding. The tanks additionally contained natural branches for enrichment. Furthermore, each family and each singly housed mouse had one running wheel, because we found in a pilot study that running wheels reduce stereotypic behavior.

Each family and each singly housed mouse had access each week for 1–2 days to an extra 70 × 50 × 35 cm enriched tank. Connection was done by removing one type 4 cage and replacing it with another type 4 cage which was connected by flexible tubes to the home tank as well as to the large enriched tank. The large enriched tank was provided with bedding, tubes and branches. Since up to five families and single mice had access to one large enriched tank on different days, mice could directly experience olfactory cues from unrelated/unfamiliar mice in these large enriched tanks.

Mice were supplied with water *ad libitum*. Striped mice in the Succulent Karoo gain a lot of weight during spring and lose more than 10% during the following dry season [22]. This might be the reason why they are very prone to extreme obesity in captivity. To avoid obesity and as a means of behavioral enrichment, mice were not fed *ad libitum*, but on the following schedule: in the morning they received a seed mix of 4.0 g/individual (guinea pig and hamster food, Haefliger AG, Herzogenbuchsee, Switzerland), at noon one piece (approx. 1.0 g) of fruit or vegetable per individual and in the afternoon two mealworms per individual.