PERGAMON

Neuroscience and Biobehavioral Reviews 23 (1999) 687–698

NEUROSCIENCE AND BIOBEHAVIORAL REVIEWS

www.elsevier.com/locate/neubiorev

Social influences on endocrine activity in guinea pigs, with comparisons to findings in nonhuman primates

Michael B. Hennessy*

Department of Psychology, Wright State University, Dayton, OH 45435, USA

Received 10 September 1998; received in revised form 2 January 1999; accepted 11 January 1999

Abstract

Guinea pigs exhibit a rich and varied social organization. Studies in recent years have demonstrated that social stimuli have widespread neuroendocrine effects in guinea pigs. Here, effects on the hypothalamic–pituitary–adrenal, adrenal medullary/sympathetic, and hypothalamic–pituitary–gonadal systems of both adult and developing guinea pigs are reviewed. These systems respond to various social variables, or factors that affect social variables, including: separation from attachment objects, housing conditions, changes in housing, the familiarity of the environment in which social interactions occur, foraging conditions, surrogate-rearing, agonistic interactions, and the establishment of dominance rank. Similarities and differences between these findings and those in nonhuman primates are discussed. It is argued that the guinea pig is well suited for the study of socioendocrine effects throughout the life span, and can provide a valuable complement to nonhuman primate research in this area.

Keywords: Social factors; Social separation; Social housing; Dominance; Hypothalamic–pituitary–adrenal; Adrenal meduallary/sympathetic; Hypothalamic–pituitary–gonadal; Guinea pig; Primate

Social behavior is intimately tied to neuroendocrine function. Not only does hormonal activity underlie or promote sexual and other forms of social behavior, but social behavior and social cues have powerful effects on neuroendocrine processes. These interactive effects serve, among other purposes, to regulate or enforce species-typical social grouping patterns and ensure successful reproduction. Much of the early work in behavioral endocrinology was driven by recognition of the profound influences that hormones could have on behavior, particularly the sexual behavior of rodents [6,61]. Although effects running in the opposite direction—influences of social behavior on endocrine activity (i.e. socioendocrine effects)—have long been known to exist (e.g. [17]), an appreciation of their pervasiveness, subtlety, and impact has grown slowly. The study of socioendocrine effects in guinea pigs is a case in point. Although much of what we know today about hormonal influences on mammalian reproduction stems from Young and colleagues' classic studies with guinea pigs in the 1950s and 1960s [102], research concerning social influences on endocrine activity in this animal is of much more recent vintage, having been published largely within the last 10–15 years. The research shows that the neuroendocrine activity of guinea pigs is exquisitely sensitive to social variables. The first purpose of the present article is to provide a comprehensive review of these findings.

A large proportion of the studies of socioendocrine effects in mammals, and many of the most exciting findings, have been with nonhuman primates. These animals are attractive as subjects because of their close phylogenetic relationship to humans. In addition, the cognitive skills of nonhuman primates, the diversity and complexity of their social structures, and the substantial background knowledge of their neuroendocrine systems make them ideal for investigating subtle social influences on endocrine activity. Nevertheless, the disproportional reliance on primates in this area also is surprising. The myriad of practical considerations that routinely impede nonhuman primate experimentation are all of major concern here. The scarcity of nonhuman primates and the expense of housing these subjects limit the number of experiments that can be performed, the number of groups that can be incorporated in an experiment, as well as the number of subjects that can be assigned to each group. Moreover, it is often necessary to use captive primates in multiple experiments. These constraints stand to compromise the power of nonhuman primate studies, and to restrict the amount and kinds of information they can provide. The extended life span of most primates relative to other common laboratory animals further slows progress,

* Tel.: +1-937-775-2943; fax: +1-937-775-3347.
E-mail address: mhennessy@wright.edu (M.B. Hennessy)

0149-7634/99/$ - see front matter
PII: S0149-7634(99)00013-5

particularly in developmental studies. With these concerns in mind, the second purpose of the present article is to examine the possible utility of the guinea pig as a rodent model to complement nonhuman primate research in the study of socioendocrine effects.

In the following section, I will present a short overview of the social organization of the guinea pig. Then studies of social influences on endocrine activity in this rodent will be reviewed, organized according to neuroendocrine system. The most common dependent measures have been circulating levels of hormones of three major neuroendocrine systems: (1) hypothalamic–pituitary–adrenal (HPA) (2) adrenal medullary/sympathetic (AMS), and (3) hypothalamic–pituitary–gonadal. These responses have been observed following an assortment of social manipulations, most frequently some form of separation from social partners or the arrangement of various, often agonistic, encounters between adult males. Although the article will focus on guinea pigs, results will be briefly compared with the main findings in other species, particularly nonhuman primates, on the same issues. This is intended first as a comparative "anchor" for the guinea pig results. The second intention is to highlight the similarities, as well as the differences, between findings in guinea pigs and primates in order to assess better the value of the guinea pig as a rodent model for socioendocrine effects. For those interested in the general psychobiology of affiliative, agonistic, and other social behavior in nonhuman primates and other species, a number of recent sources are available (e.g. [12,51,56].

1. Social structure in guinea pig groups

The guinea pig (*Cavia porcellus*) is a domestic species likely derived from the common South American rodent, *Cavia apera*. Both guinea pigs and wild cavies are gregarious animals. In the field, *C. apera* frequently feed in groups of up to nine animals, and males and females often forage together for an hour or more [69]. Further, both male and female *C. apera* have been observed to exhibit stable, linear dominance hierarchies [69]. It appears likely that young male, but not female, *C. apera* emigrate from the natal group [76]. However, detailed information of the social structure of wild cavies is not available. In the guinea pig, dominance hierarchies are often prominent in males [8,69] and have been identified in females [98]. In captive populations of multiple male and female guinea pigs, the importance of the male dominance hierarchy for social organization appears to vary with population density. At low population densities, the hierarchy seems central to the organization: Hierarchies are generally linear and stable, with the more-dominant males tending to exhibit more courtship to all resident females. At high densities, affiliative associations between individual males and females appear to be the basic unit of the organization [73]. Males form exclusive or, in some cases, shared preferences for females. Not all males succeed in forming these associations with females; the more dominant males tend to be more successful. However, this is not just an instance of dominant males achieving access to greater numbers of females than subordinate males. For one, the forming of associations can precede the gaining of dominance, at least as measured by the outcome of agonistic interactions [73]. Dominance status of males also tends to increase when a female with which the male is associated gives birth or enters postpartum estrus [73]. Thus, dominance at high population densities appears to be driven to some extent by the associations the male has formed. Moreover, at high population densities males defend territories inhabited by the females with which they associate. Dominance status of males is higher within their own territories [73].

When a small group of adult males (2–3) was examined in a large (2500 sq ft) enclosure that also contained multiple females and their offspring, dominance between the two most aggressive males was not resolved. Some territorial defense was observed, but it was incomplete at best [43]. Each of the two males tended to be more aggressive when in the vicinity of the particular shelter in which he had been placed at the beginning of the experiment, but neither male was effective in preventing the other from entering the shelter. The results of this single study, while preliminary, might be thought of as the effects of a third level of population density (extremely low) on social organization. That is, when few fully adult, competing males are present in an expansive environment, they can avoid each other so that the dominance structure described as characterizing low densities is incomplete, and males can attempt to establish territories. In sum, it may be that male dominance is the main vehicle of social organization unless the number of males become too great (as seen in the high density situation [73]), or males can avoid other dominant males (as seen in the King [43] study). When a strict male dominance hierarchy cannot readily be maintained, males attempt to establish territories, and access to females is more evenly distributed across males.

Unlike laboratory rats and mice, guinea pig pups are precocial at birth. The new born guinea pig is well furred, has its eyes and ears open, and is able to ambulate within hours. In accordance with this state of affairs, mother–infant interactions seen in guinea pigs differ in several ways from those observed in rats and mice. Maternal care in the guinea pig is quite passive and mothers do not retrieve pups. From shortly after birth, it is the pup's responsibility to maintain contact with the mother. Pups appear to be strongly motivated to follow their mother [19,58], display behavioral disturbance, including audible vocalizations, following brief, involuntary separation from her [32,59], and possibly increase their exploration of a novel environment in her presence [63]. In all, the evidence suggests that guinea pig pups display a true attachment for the mother [26]. Attachment here is viewed in the traditional sense—specifically, as an intense emotional bond to a particular individual that