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Original Investigation

Comparative quantitative investigations on brains of wild cavies (*Cavia aperea*) and guinea pigs (*Cavia aperea* f. porcellus). A contribution to size changes of CNS structures due to domestication

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ABSTRACT

Intraspecific allometric calculations of the brain to body size relation revealed distinct differences between 127 (67; 60) ancestral wild cavies and 82 (37; 45) guinea pigs, their domesticated relatives. The dependency of both measures from one another remained the same in both animal groups but the brains of guinea pigs were by 14.22% smaller at any net body weight. Consistent with results in other species the domestication of *Cavia aperea* is also characterized by a decrease of brain size. Fresh tissue sizes of the five brain parts medulla oblongata, cerebellum, mesencephalon, diencephalon and telencephalon were determined for 6 cavies and 6 guinea pigs by the serial section method. Additionally the sizes of 16 endbrain structures and those of the optic tract, the lateral geniculate body and the cochlear nucleus were measured. Different decrease values resulted for all these structures concomitant with domestication as was calculated from the amount of total brain size decrease and average relative structure values in the wild as well as the domesticated brain. The size decrease of the entire telencephalon (−13.7%) was within the range of the mean overall reduction as similarly was the case for the total neocortex (−10.7%) whereas the total allocortex (−20.9%) clearly was more strongly affected. The size decrease of the olfactory bulb (−41.9%) was extreme and clearly higher than found for the secondary olfactory structures (around −11%). The primary nuclei of other sensory systems (vision, audition) were decreased to less extent (lateral geniculate: −18.1%; cochlear nucleus: −12.6%). Mass decreases of pure white matter parts were nearly twice as high in contrast to associated grey matter parts (neocortex white versus grey matter; tractus opticus versus lateral geniculate body). The relatively great decrease values found for the limbic structures hippocampus (−26.9%) and schizocortex (−25.9%) are especially notable since they are in good conformity with domestication effects in other mammalian species. The findings of this study are discussed with regard to results of similar investigations on wild and domesticated gerbils (*Meriones unguiculatus*), the encephalization of the wild form, the special and species-specific mode and duration of domestication and in connection with certain behavioral changes as resulted from comparative investigations in ethology, socio-biology, endocrinology and general physiology.

Introduction

The domestication of animals is in general connected with a decrease of total brain size. This was ascertained through allometric comparisons of the brain size to body size relationship for a greater number of individuals of the wild progenitors versus the domesticated derivatives including different races, breeds or strains. This is valid for mammals (see reviews Herre and Roehrs 1990; Kruska 1980; Kruska 1988; Kruska 2005; Kruska 2007) and for birds as well (Ebinger 1995). Since wild living individuals of the stem species and the domesticated progeny are still of the same species (Herre and Roehrs 1990) this effect is a remarkable zoological example for intraspecific variability and plasticity of brain size. However, the dimensions of the brain size decrease due to domestication vary considerably from species to species. In eutherian mammals they range from 0% decrease (laboratory mice, Nord 1963; Frick and Nord 1963) to 34% (pigs, Kruska 1970) or approximately 35% (European cattle Kruska unpubl. observ.). Intriguingly, the brains of species at a higher level of encephalization (Carnivora, Artiodactyla, Perissodactyla) clearly are more strongly diminished in size (from 16% to 34%) due to domestication than are those of less encephalized species (Rodentia, Lagomorpha from 0% to 15%).

The results on the few domesticated rodent and lagomorph species are especially striking. From interspecific allometric

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calculations for the brain to body size relationship different encephalizations resulted for the 64 rodent and 5 lagomorph species investigated. Some species had larger, other ones smaller brains at any given body weight than the average. The wild forms of the species *Oryctolagus cuniculus* (European rabbit), *Cavia aperea* (cavy) and *Meriones unguiculatus* (Mongolian gerbil) had indices of 98, 90 and 88, respectively.They are roughly on the same but slightly on a higher encephalization level compared to the other two wild forms *Mus musculus* (house mouse) and *Rattus norvegicus* (brown rat) with values of only 66 and 62, respectively (Kruska 1980; Kruska 2005; Leybold 2000; Kruska and Steffen 2009). These indices may characterize the interspecific differences in brain sizes that resulted from species specific evolution and lifestyle adaptation during long lasting phylogenetic events. With regard to domestication and the intensity of intraspecific brain size decrease, however, a rather similar effect was recorded just for these species until today. That is – with the exception of 0% in laboratory mice and 8.7% in albinotic laboratory Wistar rats (Kruska 1975a; Kruska 1975b) – decrease values resulted to amounts of 13.1% for rabbits (Fischer 1973), 13.4% for guinea pigs (Ebinger et al. 1984), 15% for laboratory gerbils (Leybold 2000) and 12% for totally pigmented laboratory DA rats (Kruska 1988; Kruska 2005; Kruska 2007). Thus, they are of rather similar intensity. Surprisingly, this is the case although the wild species with different encephalizations are very diverse in phylogeny and lifestyle and they became domesticated at different times, at different places, for very different reasons and under different conditions (Zeuner 1963; Mason 1984; Clutton-Brock 1987; Herre and Roehrs 1990).

It was also documented for several mammal species that diverse parts of the brain are decreased in size to different degrees due to domestication. Concerning the general intensity of diminution and the sequence from lowest to highest reduction value some convergent but also divergent effects were recognized from species to species. These results additionally may point to evolutionary as well as functional and other implications (Kruska 1988; Kruska 2005; Kruska 2007). Therefore it is of interest to investigate these issues in more detail and to extend our knowledge with results on another species, *Cavia aperea*.

Cavies are endemic to the wild of South America. They are distributed in several subspecies from Venezuela over the Andes to Brazil, Paraguay, Uruguay and Argentina except for the Amazon basin and southern parts of Chile and Argentina (Hueckinghaus 1962; Eisenberg 1989; Redford and Eisenberg 1992; Eisenberg and Redford 1999; Woods and Kilpatrick 2006). Guinea pigs are descendents of cavies. They were domesticated rather early during human history compared to the other rodent species. As ascertained from archeological records they already appeared in human deposits from pre-columbian times at high altitudinal locations of nowadays Peru and Bolivia. They probably were domesticated as early as 5000 B.C. but were definitely so by 2500 B.C. Thus, they live under the domestication influence for at least 4500 years (Wing 1977; Wing 1986; Sandweiss and Wing 1997; Reitz and Wing 1999). However, since the brain size is mainly genetically determined (Weidemann 1970a; Kruska 1973; Kruska 2005; Bedi and Bhide 1988; Leybold 2000) it additionally must be recognized that guinea pigs can reproduce up to five generations per year (Trillmich 2000) and concerning the length of the domestication period they thus have lived under this influence for much more generations than have the other domesticated lagomorphs and rodents and even than the other so-called classical domesticated forms (e.g., dog, sheep, goat, cattle, pig, etc.). These were domesticated at earlier times but have a turnover of only one or two generations per year (Herre and Roehrs 1990; Zeuner 1963). Guinea pigs are still used for meat production by Andean people but world-wide they mainly serve as laboratory animals for research or as pets (Mueller-Haye 1984; Morales 1995).

Intraspecific allometric brain size to body size calculations were already performed earlier of wild cavies originally caught in Southern Peru compared with commonly used guinea pigs from breeds in Germany (Ebinger et al. 1984). This study was done by use of the total body weight and on only a limited number of 25 wild versus 37 domesticated individuals. Brain sizes of all these individuals were not included but compared with those used here. Several brain parts of three male cavies were also already determined earlier in comparison with other caviomorph rodents (Weidemann 1970b). As regards a relative brain composition of *Cavia aperea* these results are in general conformity with the results obtained here, but the investigated individuals were from a zoological garden and thus of uncertain wild origin. For this reason these data are not used here. Similarly the relative values of some brain parts given for only one guinea pig (Pirlot and Bee de Speroni 1987) were useless since no absolute data of fresh tissue are reported.

The aim of this study therefore is to re-calculate the intraspecific allometric relationship of brain to body size on new material and to determine the degree of size differences of total brain and several brain parts between wild cavies and guinea pigs.

Material and methods

Animals

Altogether 127 (67 males, 60 females) wild cavies (*Cavia aperea*) and 82 (37 males, 45 females) guinea pigs (*Cavia aperea* f. porcellus) were bred under human care at the former Institut fuer Haustierkunde of the University at Kiel. Founder individuals of the wild cavy group were in 1996 obtained from a breeding colony of Prof. Dr. Norbert Sachser, University of Muenster, Germany. They were descendants of an earlier import of individuals originally caught in the wild at the vicinity of Lujan (northern Argentina) about 60 km west of Buenos Aires. Although these wild cavies of the subspecies *Cavia aperea pamparum* are not from the Andean region and thus from the distribution area of the subspecies *Cavia aperea tschudii* where the domestication once started (Wing 1977; Wing 1986; Mueller-Haye 1984) they nevertheless are of the same species *Cavia aperea* (see Hueckinghaus 1961; Hueckinghaus 1962; Kuenzl and Sachser 1999; Kuenzl et al. 2003; Kruska and Steffen 2013; in contrast to Spotorno et al. 2006; Spotorno et al. 2007; Dunnum and Salazar-Bravo 2010). No differences in brain size occur between different subspecies of a species relative to body size (Roehrs and Ebinger 1978; Ebinger 1980). Therefore these animals can in general serve as representative for the species wild type. All the individuals used here resemble the wild cavy type of *Cavia aperea* in general appearance, size, coloration and species characteristic configuration of the upper jaw M3 in occlusal view (Hueckinghaus 1961; Hueckinghaus 1962). Guinea pigs (*Cavia aperea* f. porcellus) were bought from local breeders without any documentation of specific breeds or strains. Altogether the used individuals of this colony resemble a great variability of domesticated forms and fancy breeds with respect to outer appearance, body weight, coat color, hair structure and other features. However, they all shared the characteristic upper M3 occlusal configuration with the investigated wild cavies.

All the individuals of cavies as well as guinea pigs were kept under similar conditions as described earlier (Kruska and Steffen 2013). No interbreeding was performed between the wild and the domesticated individuals and no special breeding aims were followed within both groups. Keeping all the individuals under similar conditions was done on purpose. It seemed important to exclude or at least to equalize possible environmental and modificatory effects on the growth and size of the body as well as the brain.