of LRH whereas the effect of Pt lesions is confined to the phase of acute disruption of LRH-containing neurons. In view of the short biological half-life of circulating LRH 17, differences in the degree of induced ovarian steroidogenesis are likely. In related studies 18, it has been found that estrogen released in response to the brain stimulus is able to prime the reproductive axis for the subsequent preovulatory release of gonadotrophins.

In assessing the mode of action of various types of brain lesions on neuroendocrine tissues, it appears useful to distinguish between sites of hormone production and sites of origin of neuronal connections with hormone producing neurons. In the amygdala, opposite effects of Ss and Pt lesions on gonadotrophin release have been described 19, and such qualitative differences are to be expected in a brain structure in which lesions may either irritate or destroy synaptic inputs to hypothalamic peptidergic neurons. In the basal hypothalamus, on the other hand, different methods of brain stimulation (electrical stimulation, passage of direct current, highfrequency lesions) yield merely quantitative differences in the degree of activation of the reproductive axis 14. Our own results confirm that lesions of any type placed in areas containing LRH are likely to stimulate the pituitary-gonadal axis to varying degrees.

- 17 T. W. REDDING and A. V. SCHALLY, Life Sci. 12, 23 (1973).  $^{18}$  K. B. Ruf, M. Wilkinson and D. de Ziegler, Nature, Lond.  $257\,$ 404 (1975).
- <sup>19</sup> M. E. Velasco, Neuroendocrinology 10, 301 (1972).

### THEORIA

# Man's Strategy in Domestication - a Synthesis of New Research Trends

#### H. Hemmer

Institut für Zoologie, Johannes-Gutenberg-Universität, Postfach 3980, D–6500 Mainz (German Federal Republic, BRD), 1 December 1975.

Summary. The minimum brain size possible in the relevant wild species and certain colour types which, because of alterations in the neurotransmitter system caused by the respective colour genes, are related to behavioural traits diverging from the wild animal's norm appear to be first-rate bases for domestication either separately or in combina-

Domestication is not only an historical, but also a contemporary process. This is shown by the efforts made to use the moose (Alces alces) and the eland (Taurotragus oryx) as domestic animals<sup>1,2</sup>, as well as by the new breeding of fur-bearing animals, for example. The knowledge of how domestication starts to succeed, beyond pure description of the phenomena of domestication, has therefore not only academic but also high economic value. So one of the most urgent tasks of research in this field is to acquire a conception, practically applicable in strategies for new domestications, on the principles at work at the very starting point of former domestications, whether these occurred intentionally or by chance, and to verify this conception experimentally.

Domestication of any animal species requires that the species in question has some potential in this respect and also direct interest or at least some readiness in man to keep this animal. Compared to their previous state, there must be some changes in the man-animal relations which require changes in the wild animal's behaviour. Surely it is not accidental to find alterations usually in only one direction mainly in the sphere of the central nervous system and behaviour when observing the multiple and mostly unspecified widening of variability in domestic animals: spontaneous activity, shyness and aggressiveness towards man are commonly reduced.

These and other changes of behaviour were interpreted by Herre et al. (e.g.3) as being related to brain changes taking place at the transition from wild to domestic animals, the most conspicuous of which was supposed to be a considerable reduction of relative brain size, said to amount to between 19 and 34% in carnivores and artiodactyles<sup>3</sup>. Revisions made for two species<sup>4, 5</sup> have shown that this view is not always true, being based on methodical assumptions which cannot be maintained.

Case 1: The domestic cat. Hardly anyone believed that the domestic cat derived from the European Wildcat, but the belief in a reduction in relative brain size of about 23% from wild to domestic cat arose by comparing this form of the widespread species Felis silvestris with domestic cats<sup>3,6</sup>. The picture changes considerably on taking into account the desert-steppe cats of the northeast African and southwest Asian regions<sup>4</sup>, where the domestic cat originated, as is well known from comparative morphological studies as well as from the prehistoric doc-

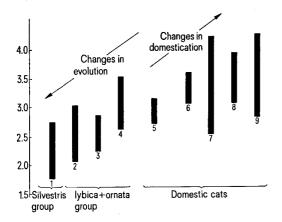
uments (e.g.<sup>3,7</sup>). The index  $\frac{\text{skull length}}{\text{braincase capacity}}$  as brought into discussion by Schauenberg<sup>8</sup> provides good information here (Figure). (This index is justified because the exponent of the length/capacity allometry does not considerably differ from isometry). Mummified cats from ancient Egypt of the first prechristian millenium<sup>12</sup> scatter, on the whole, in the range of variability of the

- <sup>1</sup> E. M. Dzhurovich and A. P. Mikhailov, Trans. First Int. Theriol. Congr. Moscow (1974), vol. 1, p. 151.
- <sup>2</sup> V. D. TREUS, N. V. LOBANOV and M. Y. TREUS, Trans. First Int. Theriol. Congr. Moscow (1974), vol. 2, p. 247.
- <sup>3</sup> W. Herre and M. Rohrs, Haustiere zoologisch gesehen (Fischer, Stuttgart 1973).
- <sup>4</sup> H. Hemmer, Experientia 28, 271 (1972).
- <sup>5</sup> H. Hemmer, Zool. Beitr. NF 21, 97 (1975).
- <sup>6</sup> M. Rohrs, Zool. Anz. 155, 53 (1955).
- <sup>7</sup> H. Petzsch, *Die Katzen* (Urania, Leipzig-Jena-Berlin 1968).
  <sup>8</sup> P. Schauenberg, Revue suisse Zool. 76, 433 (1969).
- <sup>9</sup> P. Schauenberg, Revue suisse Zool. 78, 317 (1971).
- <sup>10</sup> P. Schauenberg, Revue suisse Zool. 78, 209 (1971).
- <sup>11</sup> V. G. Heptner and E. N. Matyushkin, Zool. Zh. 51, 881 (1972).
- 12 V. G. HEPTNER and E. N. MATYUSHKIN, Zh. obshch. Biol. 34, 360

wild subspecies and show no brain size reduction at all at this level of cat domestication. Such a reduction is first traceable in cats from mediaeval Russian cities 12, where it amounts to about 10% compared with the Egyptian cats and so has already reached the mean level of contemporary domestic cats. Only the Siamese race shows some further brain size reduction of about 5 to 10%. Contrary to previous suggestions 17, this southeast Asian race originated without hybridization with other species in the same Felis silvestris basis as all other domestic cat races 18.

Case 2: The dog. Here it was the comparison of brain size of north Eurasian wolves with a modern European dog breed which lead to the assumption of an over 30% brain reduction from wolf to dog (e.g.<sup>19</sup>). Investigations in teeth morphology of dingos and central European dogs of the Roman period, as well as of wolves of different geographic origin, suggested, however, that the teeth of primitive dogs with a relatively weak and low first lower molar correspond to an early and unspecialized stage of wolf teeth evolution but not to the specialized teeth of north Holarctic wolves. Today such a primitive type of teeth is found only in the southwest and south Asian wolf populations<sup>5</sup>, in which the dog ancestors were assumed for other reasons too 20-23. The relative brain size of exactly these wolves scatters between that of north Eurasian wolves and that of dingos, as well as that of some modern dog breeds<sup>5</sup>. Moreover, the same situation exists in the central Asian steppe and desert wolf population which is the direct geographical neighbour of the southwest Asian wolves, where some specimens fall clearly in the brain size range of primitive dogs; the mean difference is only about 10% 24.

Therefore it is to be supposed that domestication occurred from the first in the populations and specimens having especially small brains in the wild species in question. A reduction in mean brain size compared to these animals may have resulted by continuing selection of this type during the early history as a domestic form. Differences between dog breeds, representing successive stages of the history of dogs, are to be explained by this principle. Dingos, presumably brought to Australia as a quasi-companion of man<sup>25</sup> in the first phase of wolf domestication, have relatively larger brains than are found in several populations of primitive but fully domesticated dogs. Such small-brained forms are the Battak



Skull length/capacity index in Felis silvestris. 1, European Wildcats; 2, African Wildcats except F. silv. lybica; 3, steppe cats of central Asia; 4, desert and steppe cats of northeast Africa to south Asia; F. silv. lybica – F. silv. ornata; 5, ancient Egypt mummified cats; 6, domestic cats from mediaeval Russian cities; 7, contemporary domestic cats; 8, Siamese cats; 9, feral domestic cats. (Data: 4, 8, 9-16)

dog, the pariah dogs, the turbary dogs of the European Neolithic, and also the Chow as an east Asian breed related to the Battak race <sup>26</sup>. Primitive dogs of the Roman period in central Europe, a basic stage for the development of later races, were still like the Neolithic ones in this respect <sup>27</sup>.

The Siamese cat, coming from the same east and southeast Asian cultural environment as the Chow, may be another example of the persistance of the original selective principle producing smaller brains compared with those of other races of domestic cats. This negative, reducing selection of brain size preceded, at least partially, other conspicuous changes in the domestic animals in question. Thus a skull of an early mediaeval domestic pig, for example, has a relative brain size as small as in modern pig breeds, but resembles in its proportions the skull of wild pigs 28. On the other hand, breeding domestic animals may also reverse the direction of this selection affecting the brain. This is shown by the example of the dog. Modern European breeds originally selected for different performances, such as herding, guarding, hunting etc., have obviously recently reached or even exceeded the dingo's brain size level in comparison with the smaller brains of their prehistoric and historic ancestors, as is evident from data published by Stephan<sup>29</sup>.

Typical differences in spontaneous activity, aggressiveness and fear of man between wild and domestic animals are not graduated in the same way as differences in relative brain size. This may be seen, for example, in comparing European and African Wildcats, typical domestic cats, Persian cats and Siamese cats. Some studies on motility made in a research course conducted by the author confirm the wellknown low spontaneous activity of Persian cats vs. European shorthaired cats and crossbreeds between the two races. The relative braincase volume of a primitive Angora, as well as of a modern Persian cat so far measured, are the same as the mean of other domestic cats. The Siamese cat, known to be usually especially lively, is characterized by a somewhat smaller brain on the average than the above races. African Wildcats of the east and south African subspecies group have a smaller mean brain size than European Wildcats and are usually less aggressive towards man in captivity and more easily tamable. In mice, the whole scale from wild to domestic animals is found without any differences in brain size at all 30.

- $^{18}$  J. Kratochvil and Z. Kratochvil, Zool. Listy 19, 293 (1970).
- <sup>14</sup> P. J. H. VAN BREE, R. W. M. VAN SOEST and J. C. M. VETTER, Publ. natuurhist. Genootsch. Limburg 20, 11 (1970).
- <sup>15</sup> P. DERENNE, Mammalia 36, 459 (1972).
- <sup>16</sup> J. Sladek, A. Mosansky and J. Palasthy, Zool. Listy 20, 153 (1971).
- 17 H. L. BLONK, Wilde Katten (Thieme, Zutphen 1963).
- <sup>18</sup> H. Hemmer, in preparation.
- <sup>19</sup> W. Weidemann, Z. Säugetierk. 35, 238 (1970).
- $^{20}$  E.-L. Trouessart, C. r. Acad. Sci., Paris  $152,\,909$  (1911).
- <sup>21</sup> Т. Noack, Zool. Anz. 46, 75 (1915).
- <sup>22</sup> A. Brinkmann, Vidensk. Meddr. dansk naturh. Foren. 72, 1 (1921).
- <sup>23</sup> J. Clutton-Brock, Z. Tierzücht. ZüchtBiol. 76, 326 (1962).
- 24 H. HEMMER, in preparation.
- <sup>25</sup> N. W. G. Mac INTOSH, in *The Wild Canids* (Ed. M. W. Fox; Van Nostrand Reinhold, New York-Cincinnati-Toronto-London-Melbourne 1975), p. 87.
- <sup>26</sup> P. LÜPS and W. HUBER, Mitt. naturforsch. Ges. Bern NF 28, 16 (1971).
- <sup>27</sup> H. HEMMER and M. EICHMANN, Mainzer naturwiss. Arch. 11, 257 (1972)
- <sup>28</sup> A. Oelbermann, unpubl. dipl. work (1974).
- <sup>29</sup> H. Stephan, Zool. Anz. 153, 15 (1954).
- <sup>80</sup> H. FRICK and H. J. NORD, Anat. Anz. 113, 307 (1963).

Effects of chronic chlordiazepoxide treatment on Cotton Rats

|                                    | Controls                | Drugged animals  |
|------------------------------------|-------------------------|------------------|
| Escape response                    | Strong                  | Weak             |
| Aggressiveness                     | High                    | Hardly existent  |
| Social contacts                    | Strong                  | Weak             |
| Integration of strangers in groups | Usually hardly possible | No difficulties  |
| Choice of nesting place            | With some cover         | Almost at random |
| Defence of nesting territory       | Vigorous                | Lacking          |
| Average litter size                | 4–5                     | 6–7              |
| Weight at the age of 5 months      | About 175 g             | About 250 g      |

Behavioural changes of this type can be produced in model experiments with rodents by chronic psychopharmacological manipulations of the neurotransmitter system. With this aim, studies on the Cotton Rat (Sigmodon hispidus) were carried out in the laboratory of the author by Ernst<sup>31</sup>. This American species usually shows high intraspecific aggressiveness and a high level of fearfulness, which suit it for testing tranquillizing agents 32. The test and control animals were housed in groups of 4 or more individuals and were fed with a homogeneous mixture of commercial food pellets, bananas and dextrose. With this food the test rats got chlordiazepoxide (Librium) over the whole experimental time of several months in the same average dose per kg per day. The escape response was tested with a standardized air blast; other reactions were recorded according to their frequency. In the first week of the drug the escape response progressively diminished: the escape jump originally reaching an average height of 20 cm totally disappeared, the response duration dropped from 3 sec to 1 sec and remained constant at this level, and the escape run was reduced from 75 to about 10 cm. The frequency and the intensity of body contacts with other individuals at rest was diminished to nearly half of that in the controls. Halfgrown rats especially tended more and more to social isolation in the cage corners. The frequency of serious fights was likewise drastically reduced. No more biting was observed from the middle of the second week on. Usually it is impossible to integrate strangers in a group of Cotton Rats 33, but this could be achieved in the drugged animals without any difficulties. Whereas the control mothers immediately attacked other members of their group which came within a reach of about 10-15 cm around their nesting place, the drugged ones tolerated other animals in the immediate vicinity of the nest. This behaviour resulted in one case in social resting straight after birth of the young, so that most of them were crushed to death or pushed from the nest. Normal females construct their nests in places with some cover, e.g. in the corners of the cage, the test females built them more at random, even in the middle of the cage. The usual separation of eating, resting and defecation sites was cut out. The drugged rats became heavier than the controls: animals born during the experiment weighing about 40% more than controls at the age of 5 months. The litter size amounting to 4-5 (mean of 9 litters) in control Cotton Rats housed in groups increased in the test animals to 6-7 (mean of 10 litters). Altogether this chronic drug application produced a behavioural and developmental complex with reduced escape response and aggressiveness, marked indifference to conspecifics, deficiency in the care of young, increase in descendant number and in body weight, as is typical, on the whole, for domestic animals compared with their wild ancestors.

Such alterations in the neurotransmitter system, which these experiments show to be a basis for bahavioural changes typical for the transition from the wild to the domesticated state, can be found, for example, when comparing different strains of laboratory mice and rats, as proved by several papers especially from the psychopharmacological field in the last years (e.g. 34-36). In the normal behaviour not affected by drugs, differently coloured laboratory rodent strains also show differences especially in the complexes changed by domestication. This is well known for the laboratory mouse, where the albino animals seem to have a higher level of domestication than the black ones, if compared with wild mice of the same species 37. An examination of the exploratory activity, which is inversely related to shyness, showed the responsiveness of albino mice to novel objects as significantly larger than that of black ones, which in turn react more than wild mice kept under the same conditions 38. Preliminary behavioural tests and crossbreeding with wild and albino domestic rats confirm the difference in spontaneous activity of both forms, as described by RICHTER 39. The mean motility of F<sub>1</sub> hybrids ranges between the respective scores found for the parental groups. In F, hybrids the white ones behaved like the original albinos in general, whilst the motility score of the animals coloured like wild rats, or like F2 hybrids, scattered in the range of the F<sub>1</sub> animals. An effect of the albino gene upon the behaviour of mice was described by Fuller 31. Such psychosomatic correlations, as recently referred to by Trumler 40 in discussing domestication problems, were thoroughly studied with quantitative behavioural and biochemical tests by Keeler<sup>41</sup> in rats, mink and red foxes. He came to the important conclusion that 'it appears certain that adrenal and thyroid functions are altered by the presence of coat color genes and that through these altered functions, fear is modified'.

 $^{\rm 31}$  H. Ernst, unpubl. dipl. work (1972).

<sup>32</sup> G. Vogel and L. Ther, Arzneimittelforschung 10, 806 (1960).

33 H. HEMMER, Zool. Anz., Suppl. 33, 306 (1970).

J. L. Fuller, Anim. Behav. 15, 467 (1967).
 K. M. Taylor and R. Laverty, Eur. J. Pharmac. 17, 16 (1972).

- <sup>37</sup> I. Eibl-eibesfeldt, Z. Tierpsychol. 7, 558 (1950).
- <sup>38</sup> C. Diehl, unpubl. dipl. work (1971).

<sup>39</sup> C. P. Richter, J. natn. Cancer Inst. 15, 727 (1954).

<sup>40</sup> E. TRUMLER, Mit dem Hund auf Du (Piper, München 1971).
 <sup>41</sup> C. KEELER, in The Wild Canids (Ed. M. W. Fox; Van Nostrand Reinhold, New York-Cincinnati-Toronto-London-Melbourne 1975), p. 399.

<sup>&</sup>lt;sup>36</sup> R. J. BARRETT, N. J. LEITH and O. S. RAY, Behav. Biol. 11, 189 (1974).

Correlations of this type, i.e. coat colours clearly differing from the normal look of the wild animals related to behavioural changes in the direction typical for domestic animals, certainly have first rank importance as starting points for domestication achieved by chance as well as by intention. Prey animals marked by a highly unusual colour may give rise to alterations, eventually inhibition of the hunting behaviour in carnivores which rely chiefly on vision, as shown for wild kestrels having the choice between wild type coloured and albino mice 42. A comparable behavioural change in man may easily result in relation to an animal externally and beaviourally marked in such an unusual manner as the first step towards the change in the man-animal relation decisive for a domestication, especially if such animals become objects of myths or cult interest in any way.

A clear example for such differentiated human handling resulting in all probability in the domestication of the Norway Rat, is given by reports on the rat-baiting sport popular in France and England around 1800, and in America soon afterwards 38. As communicated by RICHTER 38, records indicate that albinos were removed from the large numbers of wild rats trapped for this purpose, that is, being killed in groups of 100 to 200 individuals by a trained terrier in a fighting pit in as short a time as possible. These albinos were then kept for show purposes and /or breeding. Obviously a similar coulor selection took place at the very starting point of the wolf's domestication. The genes responsible for the normal wolf colour seem to be completely lacking in the dingo 3. Likewise, red, yellow and other 'dog' colours are found in primitive dogs from wolf-free regions where the 'wolf'

colour hardly occurs at all. Therefore it can be assumed that the dog's history is founded on a very limited number of wolves coloured in this unusual manner such as are found now and then in some wolf populations. The author had the opportunity to examine such a dingo-coloured skin of a Kazakhstan steppe wolf, for example, when visiting the Zoological Institute of the Kazakh Academy of Sciences in Alma-Ata.

Two factors, namely certain colour types which, because of alterations in the neurotransmitter system caused by the respective colour genes, are related to behavioural traits diverging from the wild animal's norm, and secondly the minimum brain size possible in the relevant species, therefore appear to be bases for domestication either separately or in combination. These factors are expressions of the respective individual's potentiality for domestication as well as being at least partially decisive for man's readiness to keep this animal, as shown by the example of the albino rat. Future domestication research will have to examine the general validity of this thesis. Understood as a domestication strategy, its application should result in success more quickly than if only general selection of individuals, according to their docile, tractable behaviour<sup>43</sup>, is undertaken. In addition, primary selection procedures referring to relative brain size must be prepared.

- 42 H. HEMMER and H. MOHRDIEK, in preparation.
- <sup>48</sup> D. K. BELYAEV and L. N. TRUT, in *The Wild Canids* (Ed. M. W. Fox; Van Nostrand Reinhold, New York-Cincinnati-Toronto-London-Melbourne 1975), p. 416.

### PRO EXPERIMENTIS

## A Simple System for Mechanical and Electrical Recordings from Frog Nerve-Muscle Preparation

M. Licker, B. Lange and A. Pabst<sup>1</sup>

Institut für Tierphysiologie und Angewandte Zoologie der Freien Universität Berlin, Grunewald Strasse 34, D-1 Berlin 41 (German Federal Republic, BRD), 15 October 1975.

Summary. A device is described which can be used for simultaneous measurement of the muscle action potential and the contraction of the frog gastrocnemius nerve-muscle preparation. The apparatus is characterized by ease of construction, good accuracy and reliability.

We required for use in an introductory physiology laboratory course, a system for recording the contractions as well as the action potentials (MAP) of the frog gastrocnemius nerve-muscle preparation. For didactic reasons it was important to be able to demonstrate and measure the latency and time course of the mechanical event in relation to the MAP. Other requirements were ease and clarity of use and reliability in the student laboratory. We could not justify for this one experiment the purchase of a commercially available dual channel system, especially since several groups were to work simultaneously. We therefore designed and built the following recording apparatus, based on a commercially available linear motion transducer, for use in conjunction with a cathode ray oscilloscope.

The device (see Figure 1) is fabricated for the most part from plexiglas. It contains a shallow moist chamber with a removable cover (not shown in the figure) with provisions for holding the preparation, for nerve stimulation and for recording the MAP (Figure 1A). The conventional-

ly prepared nerve-muscle preparation is held by the Tshaped holder whose position can be adjusted by loosening its retaining screw and sliding the stalk in or out. The stumps of the femur and tibia should not be cut too short. By inserting the head of the muscle at its attachment to the bone into the notch in the holder with both bone stumps behind the head of the T, the muscle can be held firmly for recording. Care should be taken to avoid pinching the nerve between the bone and the plexiglass. The nerve is laid over the 0.7 mm silver stimulating electrodes which are mounted in an adjustable stalk held by a thumb screw. The 2 recording electrodes are thin silver wires, 0.25 mm in diameter, which are simply twisted around the belly and tendon of the muscle. Since they have to be replaced occasionally, they are fastened to miniature, removable banana jacks held in the frame by screws (see top view diagram for details of the holder and

<sup>&</sup>lt;sup>1</sup> We thank Ms. C. Friedemann for preparation of the drawings; Ms. A. Middelmann for technical assistance.