



Figure 9.11. Diagram illustrating the percent reduction of brain subdivision volumes in domesticated mallard compared with the wild form. Arrow line indicates the percent decrease in total brain volume. (Modified from Ebinger, 1995.)

Measurements of multimodal integration centers (i.e., neostriatum and ventral hyperstriatum), demonstrate a reduction as well. There is evidence, however, that this depends on the breed studied. Interestingly, in homing pigeons, these areas do not seem to be reduced as much as in other breeds. The homing ability of homing pigeons is a multimodal cognitive phenomenon (Papi, 1991, 1995; Bingman et al., 1994, 1995). One would expect multimodal areas to be particularly large in homing pigeons. Our data on brain composition in this breed compared with nonhoming breeds show that neostriatum with its large multimodal integration centers contributes to a larger degree to the telencephalon in homing than in the nonhoming breeds.

Similar values have been calculated in chickens of the breed Japanese Chabos (Rehkämper et al., 1995). Here, too, a larger neostriatum is found compared with chickens of the breed Silky hens. For these chickens, behavioral data are not yet available, but the first Skinner-box experiments point to remarkable cognitive capacities of Chabos, including categorical or conceptual behavior.

Cognitive capacities of domestic animals deserve more attention. Generally, the brains of domesticated animals are smaller than those of the wild forms. This, however, does not necessarily mean that all brain parts undergo a reduction. Klatt (1921) has suggested that brain parts engaged in associative learning might be larger in domesticated species than in their wild ancestors. It is probable that domesticated animals need special cognitive abilities to live together with humans, because association with a different species may require different communication skills. This may

well be the central point of the domestication problem. There are data that support this idea. Some breeds of dogs (e.g., poodles) that live closely with humans are unable to organize social systems among themselves. When a human is integrated, however, the situation changes, and an effective system is built up that includes the human (Feddersen-Petersen, 1994). This could be viewed as a problem of cognition, which has been solved by the domesticated animal through superior learning capacities. Thus, it might be that reduction of telencephalic size in the course of domestication is accompanied by progressive development of cognitive abilities. On the other hand, it could be that humans impose the organization, and the poodles no longer need their own abilities. Clearly, this idea needs to be further tested.

AGAIN: THEORIES OF BRAIN SIZE AND BRAIN COMPOSITION

We presented our data in a way that they support the adaptationist hypothesis. The reduction of the visual cortex in *Spalax* together with an enlargement of the somatosensory representation areas could be explained in this way. The data on domesticated animals also offer support for this hypothesis. Selection pressures that led to the current configurations for wild animals are largely unknown; those that selected domesticated animals are known. Thus, they can be seen as a sort of experiment to visualize brain plasticity and the selective pressures that can change brain shape. We now would like to come back to the initially presented hypotheses of brain size alteration and discuss them against the background of our own data and thoughts.

The arguments of Roth et al. (1994) that genome size can determine brain size and complexity independent of functional considerations and of Clayton and Krebs (1994) that experience plays a role in determining the size of brain parts cannot be discussed adequately within the framework of our approach, because we do not have appropriate data. Particularly, the impact of individual learning processes on morphometry of the brain would be very interesting to investigate further: Homing pigeons, for example, would be a good model to test their hypotheses.

The variation seen in brain composition is not in agreement with the isometry hypothesis (all brain parts increase to the same degree) as formulated by Jerison (see above). This theory could not predict the reduction of visual cortex in *Spalax*, and it does not come to grips with what is seen in pigeon or chicken breeds. Previously, Fox and Wilczynski (1986) showed that somatic brain regions, which are necessary "to maintain vegetative, sensorimotor, and related behavior," for example, the spinal cord and the brain stem, scale by a different exponent of body weight than nonsomatic brain regions, for example, forebrain and cerebellum. Frequently, individual parts of the brain are found to scale against body weight with different slopes (Stephan et al., 1991; Rehkämper et al., 1991a). All these data do not support Jerison's chain of arguments. In addition, Holloway (1979) points out that it is not neural mass alone that is important, but the internal organization of the brain, which he calls "wiring." This would also be true for functional subparts of the brain as measured in Stephan's

studies or in the present Chapter. Unfortunately, the wiring is much more difficult to study in living animals and impossible in fossils, which play an important role in Jerison's work.

Jerison (1985) seems to be aware of such problems, but he points out that focusing on the isocortex alone (i.e., on an isolated brain part), might underevaluate the olfactory-guided "intelligence," one type among many that he recognizes. These different types of intelligence, however, need to be defined more clearly. Otherwise, every activity of the nervous system would be, in a way, intelligent, and the term would lose any heuristic value.

The data of Armstrong (1985; see above) on brain size in prosimians, in comparison with monkeys, are difficult to understand in biological terms. To us, it seems unreasonable to assume that prosimians and monkeys are neurobiologically identical. The same can be said for passerine and nonpasserine birds, which have been compared by Armstrong and Bergeron (1985). In neither case is there any behavioral and psychological data to support that equality.

Deacon (1990; see above) proposed a displacement theory that seems to integrate some other concepts (e.g., Ebbesson's parcellation theory). It is assumed that competitive axonal interaction during ontogenesis leads to a loss of connections, or acquisition of additional connections, or replacement of one class of connections by another. As a consequence, morphometric alterations occur. Deacon's introduction to his theory (1990) included a demand for functional analysis. The living animal in its environment is not, however, a part of his theory. This is illustrated clearly when he argues, "Multiplication of cortical areas might be accounted for, not as augmentation of function, but as response to a growing size differential. This must certainly be a rich source for 'preadaptation'." (Deacon, 1990, p. 685).

For us, the crucial point in evolutionary biology is not only to ask how brains acquired their typical size and shape, but, even more important, to ask what an animal can do with such a brain to survive. This is where selection comes in. Problems of phylogeny, as discussed by Deacon (1990), are not in the center of interest of evolutionary neurobiology. It is illuminating when Gould (1975) states that interspecific comparison in neuromorphometry "is by far the worst to consult for information about evolutionary mechanisms. It represents the static scaling of contemporary adults within a group; it is not the result of ancestral-descendant sequences among the forms constituting it. It provides scaling criteria for the functional morphologist, but it does not represent the path traveled by an organism towards that adaptation" (p. 277). For us, evolutionary research in the post-Darwinian era is much closer to functional morphology than to phylogeny. This has to do with the actualistic strategy of Darwin (Rehkaemper, 1997), as it must be. Functional morphology is observable in the present time, phylogeny only in the past.

Deacon and others criticized Stephan and collaborators for being trapped in *scala naturae* thinking. We regard that as a superficial interpretation. This argument seems to be made automatically whenever scaling is an obvious method of analysis. Scaling is, however, nothing more than a simple approach to sorting morphometric data in an objective and reproducible manner. It enables us to find species that deviate from some predicted values. Such species are "hot spots" that might be examined in greater

detail. There is no hidden philosophy in such calculations, except the conviction that there is an underlying relationship in the various measurements of brain and body size. Hot spots are of interest for the evolutionary neurobiologist because they might indicate particularly strong selective pressures and stimulate fruitful research on the biology of an identified species.

The position of Deacon (1990) is not necessarily contradictory to the points of view of Finlay and Darlington (1995; see above) as far as the influence of ontogenesis is concerned. These authors argue that (1) the length of neurogenesis defines the size of the brain and that (2) in the end, the sizes of brain parts in different brains can be predicted if the size of the total brain is known. Whereas the condition of the adult brain may well be influenced by the mode of development, we can hardly imagine that this developmental factor is neutral to adaptation and selection. It should also be noted that their first assertion is true only if the "rate" of neurogenesis is constant across species.

Finlay and Darlington's second point (1995) is not immune from two methodological problems shared by many scaling studies. First, there is no doubt that their calculations are correct. One might ask, however, if it is biologically acceptable to calculate "mouse to elephant" curves. When the body weight range is large, it is expedient to use double logarithmic plots, making it look as if the data points (brain size, brain part size) are very near the line. This gives the impression that no differences (or at least only small differences) exist. Because in such calculations many species are represented by a limited number of individuals, there is an insufficient database to test differences statistically. This, however, is not a proof of uniformity. One example helps visualize this point. Finlay and Darlington (1995, their Fig. 1) stress the point that there is a linearity in the relation of iso(neo)cortical size and brain size in insectivores, prosimians, simians, and bats. At first glance it looks as if the isocortex of the largest insectivore, *Solenodon*, is similar in size to that in the small simian *Cebuella*. Because in these two species brain size is nearly identical, they may be compared directly. The isocortex of *Solenodon* measures 661 mm³ and that of *Cebuella* 2.535 mm³. Thus, the *Cebuella* brain, which is similar in size to that of *Solenodon*, bears an isocortex approximately four times larger. We think this difference is biologically important.

Second, the slopes of subgroups might be significantly different from the overall slope. Harvey (1988) and Healy and Harvey (1990) have calculated such slopes for different groups that are defined as systematic entities or nutritional groups. They clearly demonstrated that such groups do have different slopes. Mann et al. (1988) have described the same phenomenon. Following the ideas of Rempe (1962), Rempe and Weber (1972), and Hofmann (1982), Rehkaemper et al. (1991c) demonstrated a mathematical method for dealing with this problem. They compared brain and body sizes in hummingbirds and galliform birds. Hummingbirds are extremely small, whereas galliform birds may reach remarkable sizes. Shifting the data to a common origin and standardizing the variances allows one to calculate a slope that adequately describes brain size-body size relationships in both groups. This slope can be used for comparison after the data have been transferred back to the original position before variances were standardized.

CONCLUSIONS

Evolution is understood as functional adaptation. This concept has been used to deal with large telencephala found in some species of both mammals and birds. It emphasizes the necessity of considering the functional heterogeneity of the telencephalon in attempting to understand its size from a biological point of view.

Methodologically, an allometric approach that takes body weight into consideration is favored. This helps to identify the impact of the body on the brain and, thus, to differentiate brain evolution from independent evolution of body size as is seen sometimes.

In mammals, large telencephala may be associated either with voluminous olfactory cortices or with expanded hippocampi. Large isocortices are generally found in animals with large telencephala. Again, biologically relevant specializations such as large somatosensory systems or large motor systems have been evolved. Often, parts of the isocortex associated with cognitive functions have been enlarged disproportionately.

Variability in telencephalic size typical of mammalian brains is likewise found in avian brains, although birds have not been studied to the same extent. Many data support the hypothesis that, in the avian brain, the neostriatum and hyperstriatum complex plays the role of the mammalian isocortex. Within this complex, large areas have the infrastructure for cognitive capacities, and there is strong evidence that birds likewise exhibit a trend toward a volumetric increase in the size of structures that serve cognition. Among the birds, passeriform species occupy a leading position.

Thus, birds and mammals show a parallelism in evolutionary trends that leads to analogies (or homoplasies and convergences) in brain organization. In Darwinian terms of evolution, such analogies are probable. If one group has found a strategy that appears to be of biological advantage, it is likely that other groups will use this advantage as well. Examples are glossophagine bats and hummingbirds. Both groups make use of nectar, and the key to this biology is hovering flight. To this end, extrapyramidal motor areas such as cerebellum, nucleus ruber, and inferior olive are allometrically enlarged (Stiefken, 1993; Kinkel, 1994).

Domestication is evolution under man-made constraints. In this special case, cognitive abilities might play a crucial role. However, we are far from having satisfying data about either cognitive capacities or the brain structures associated with cognition.

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REFERENCES

- Armstrong, E. (1982) A look at relative brain size in mammals. *Neurosci. Lett.* 34:101-104.
- Armstrong, E. (1983) Metabolism and relative brain size. *Science* 220:1302-1304.
- Armstrong, E. (1985) Relative brain size in monkeys and prosimians. *Am. J. Phys. Anthropol.* 66:263-273.
- Armstrong, E., and R. Bergeron, (1985) Relative brain size and metabolism in birds. *Brain Behav. Evol.* 26:141-153.
- Ax, P. (1987) *The Phylogenetic System. The Systematization of Organisms on the Basis of Their Phylogenesis.* J. Wiley & Sons, New York.
- Bang, B.G. and S. Cobb (1968) The size of the olfactory bulb in 108 species of birds. *Acta 85:55-61.*
- Baron, G., H. Stephan, and H.D. Frahm, (1996) *Comparative neurobiology in chiroptera*, vols. 1-3. Birkhäuser, Basel.
- Benjamini, L. (1983) Studies in the learning abilities of brown necked ravens and herring gulls. I. Oddity learning. *Behaviour* 84:173-194.
- Bingman, V., G. Casini, C. Noejar, and T.-J. Jones, (1994) Connections of the piriform cortex in homing pigeons (*Columba livia*) studied with fast blue and WGA-HRP. *Brain Behav. Evol.* 43:206-218.
- Bingman, V.P., T.-J. Jones, R. Strasser, A. Gagliardo, and P. Ioalé (1995) Homing pigeons, hippocampus and spatial cognition. In E. Alleve, A. Fasolo, H.P. Lipp, L. Nadel, and L. Ricceri, (eds.): *Behavioural Brain Research in Naturalistic and Semi-Naturalistic Settings: Possibilities and Perspectives.* Kluwer, Dordrecht, pp. 207-224.
- Boite, D., and G. Baron, (1994) Allometric comparison of brain and main brain subdivisions in birds. *J. Brain Res.* 35:49-66.
- Bowler, P. (1996) *Life's Splendid Drama.* University of Chicago Press, Chicago.
- Bronchti, K. (1909) *Vergleichende Lokalisationslehre der Großhirnrinde.* Ambrosius Barth, Leipzig.
- Bronchti, G., N. Schönberger, E. Welker, and H. van der Loos, (1992) Barrel field expansion after neonatal eye removal in mice. *Neuroreport* 3:489-492.
- Chapin, J.K., and C.S. Lin, (1984) Mapping the body representation in the SI cortex of unanesthetized and awake rats. *J. Comp. Neurol.* 229:199-231.
- Clayton, N., and J. Krebs, (1994) Hippocampal growth and attrition in birds affected by experience. *Proc. Natl. Acad. Sci. U.S.A.* 91:7410-7414.
- Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection.* Murray, London.
- Deacon, T. (1990) Rethinking mammalian brain evolution. *Am. Zool.* 30:629-705.
- Delius, J.D. (1992) Comparative cognition of identity. In P. Bertelson, P. Eelen, and G. d'Ydewalle, (eds.): *International Perspectives on Psychological Science, vol., Leading Themes.* Lawrence Erlbaum, Hillsdale, NJ, pp. 25-40.
- Dubois, E. (1897) Über die Abhängigkeit des Hirngewichts von der Körpermasse bei den Säugethieren. *Arch. Anthropol.* 25:1-28.
- Ebbesson, S.O.E. (1980a) The parcellation theory and its relation to interspecific variability in brain organization, evolutionary and ontogenetic development and neuronal plasticity. *Cell Tissue Res.* 213:179-212.
- Ebbesson, S.O.E. (ed.) (1980b) *Comparative Neurology of the Telencephalon.* Plenum, New York.
- Ebinger, P. (1974) A cytoarchitectonic volumetric comparison of brains in wild and domestic sheep. *Z. Anat. Entwickl. Gesch.* 144:267-302.
- Ebinger, P. (1975a) A cytoarchitectonic volumetric comparison of the area gigantopyramidalis in wild and domestic sheep. *Anat. Embryol.* 147:167-175.
- Ebinger, P. (1975b) Quantitative investigations of visual brain structures in wild and domestic sheep. *Anat. Embryol.* 146:313-323.
- Ebinger, P. (1995) Domestication and plasticity of brain organization in mallards (*Anas platyrhynchos*). *Brain Behav. Evol.* 45:286-300.
- Ebinger, P. (1996) Domestikationsbedingte Änderungen von Hirn und Verhalten beim Hausgeflügel. In G. Rehkämper, and H. Greven, (eds.): *Beiträge zur Biologie der Haus- und Nutztiere. Acta biol. benrodis*, Suppl. 3, Verlag Natur & Wissenschaft, Solingen pp. 37-52
- Ebinger, P., and R. Löhmer, (1987) A volumetric comparison of brains between greylag geese (*Anser anser L.*) and domestic geese. *J. Hirnforsch.* 28:291-299.
- Ebinger, P., G. Rehkämper, and H. Schröder, (1992) Forebrain specialisation and the olfactory system inanseriform birds. *Cell Tissue Res.* 268:81-90.

- Ebinger, P., and M. Röhrs. (1995) Volumetric analysis of brain structures, especially of the visual system in wild and domestic turkeys (*Melaneris gallopavo*). *J. Brain Res.* 36:219-228.
- Eldredge, N., and J. Cracraft. (1980) *Phylogenetic Patterns and the Evolutionary Process*. Columbia University Press, New York.
- Feddersen-Petersen, D. (1994) Ethologische Untersuchungen zu Fragen des Normalverhaltens, zur Ermittlung sozialer Umweltansprüche und zur Präzisierung des Begriffes der "tiergerechten Haltung" von Haushunden. *Klientierpraxis* 39:659-684.
- Finlay, B.L., and R.B. Darlington. (1995) Linked regularities in the development and evolution of mammalian brains. *Science* 268:1578-1584.
- Fox, J.H., and W. Wileczynski. (1986) Allometry of major CNS divisions: towards a reevaluation of somatic brain-body scaling. *Brain Behav. Evol.* 28:157-169.
- Frahm, H.D., G. Rehkämper, and E. Nevo. (1997) Brain structure volumes in the mole rat, *Spalax ehrenbergi* (Spalacidae, Rodentia) in comparison to the rat and subterranean insectivores. *J. Brain Res.* 38:209-222.
- Gahr, M. (1997) How should brain nuclei be delineated? Consequences for developmental mechanisms and for correlations of area size, neuron numbers and functions of brain nuclei. *TINS* 20:58-62.
- Gould, S.J. (1975) Allometry in primates, with emphasis on scaling and the evolution of the brain. In F. S. Szalay (ed.): *Approaches to Primate Paleobiology*. Karger, Basel, pp. 244-292.
- Günürkün, O. (1997) Cognitive impairments after lesions of the neostriatum caudolaterale and its thalamic afferents in pigeons: functional similarities to the mammalian prefrontal system? *J. Brain Res.* 38:133-143.
- Harvey, P. (1988) Allometric analysis and brain size. In H.J., Jerison and I. Jerison (eds.): *Intelligence and Evolutionary Biology*. NATO ASI Series G 17. Springer, Berlin, pp. 199-210.
- Harvey, P., and J.R. Krebs (1990) Comparing brains. *Science* 249:140-146.
- Healy, S. D., and P. Harvey (1990) Comparative studies of the brain and its components. *Neth. J. Zool.* 40:203-214.
- Hennig, W. (1966) *Phylogenetic Systematics*. University of Illinois Press, Urbana.
- Herre, W., and M. Röhrs (1990) *Hausiere-zoologisch gesehen. 2. Auflage*. Fischer, Stuttgart.
- Hofman, M.A. (1982) Encephalization in mammals in relation to the size of the cerebral cortex. *Brain Behav. Evol.* 20:84-96.
- Holloway, R.L. (1979) Brain size, allometry, and reorganization: towards a synthesis. In M.E. Hahn, et al. (eds.): *Development and Evolution of Brain Size: Behavioral Implications*. Academic Press, New York, pp. 59-88.
- Jacobs, L.F., and W.D. Spencer. (1994) Natural space-use patterns and hippocampal size in kangaroo rats. *Brain Behav. Evol.* 44:125-132.
- Jerison, H.J. (1955) Brain to body ratios and the evolution of intelligence. *Science* 121:447-449.
- Jerison, H.J. (1973) *Evolution of the Brain and Intelligence*. Academic Press, New York.
- Jerison, H.J. (1977) The theory of encephalization. *Ann. N.Y. Acad. Sci.* 299:146-160.
- Jerison, H.J. (1985) Animal intelligence as encephalization. *Philos. Trans. R. Soc. Lond. Biol.* 308:21-35.
- Jerison, H.J. (1994) Evolution of the brain. In D.W. Zaidel, (ed.): *Neuropsychology. Handbook of Perception and Cognition*. Academic Press, San Diego, pp. 53-82.
- Jolicoeur, P., and A.A. Heusner. (1971) The allometry equation in the analysis of the standard oxygen consumption and body weight of the white rat. *Biometrics* 27:841-855.
- Kaas, J.H. (1991) Plasticity of sensory and motor maps in adult mammals. *Annu. Rev. Neurosci.* 14:137-167.
- Källén, B. (1951) Embryological studies on the nuclei and their homology in the vertebrate forebrain. *Kgl. fysiogr. Sällsk. Lund Handl. N.F.* 62, 5:1-36.
- Källén, B. (1962) II. Embryogenesis of brain nuclei in the chick telencephalon. *Erg. Anat. Entwickl.* 36:62-82.
- Karten, H.J. (1965) Projections of the optic tectum of the pigeon (*Columba livia*). *Anat. Rec.* 151:369.
- Karten, H.J. (1968) The ascending auditory pathway in the pigeon (*Columba livia*). II. Telencephalic projections of the nucleus ovoidalis thalami. *Brain Res.* 11:134-153.
- Karten, H.J. (1969) The organization of the avian telencephalon and some speculations on the phylogeny of the amniote telencephalon. *Ann. N.Y. Acad. Sci.* 167:164-179.
- Karten, H.J. (1979) Visual lemniscal pathways in birds. In A.M. Granda, and J.H. Maxwell (eds.): *Neural Mechanism of Behavior in the Pigeon*. Academic Press, New York, pp. 409-430.
- Karten, H.J. (1991) Homology and evolutionary origins of the neocortex. *Brain Behav. Evol.* 38:264-272.
- Karten, H.J., and J.L. Dubbeldam. (1973) The organization and projections of the palaeostriatal complex in the pigeon (*Columba livia*). *J. Comp. Neurol.* 148:61-90.
- Karten, H.J., and Hodos, W. (1970) Telencephalic projections of the nucleus rotundus in the pigeon (*Columba livia*). *J. Comp. Neurol.* 140:35-52.
- Kinkel, H. (1994) *Vergleichend-allometrische Untersuchungen zur Volumenfüllung von Kerngebieten im Hirnstamm von Hühner- (Galliformes), Singvögel (Passeriformes) und Kolibris (Trochilidae)*. Dissertation, Med. Fakultät, Universität Köln.
- Klatt, B. (1921) *Studien zum Domestikationsproblem. Untersuchungen am Hirn. Bibliotheca genetica*, Band II. Borntraeger, Leipzig.
- Kleiber, M. (1961) *The Fire of Life*. Wiley, New York
- Krebs, J., D.F. Sherry, S.D. Healy, V.H. Perry, and A.L. Vaccarino (1989) Hippocampal specialisation in food storing birds. *Proc. Natl. Acad. Sci. U.S.A.* 86:1388-1392.
- Kruska, D. (1970) Über die Evolution des Gehirns in der Ordnung Artiodactyla Owen 1848, insbesondere der Teilordnung Suina Gray 1868. *Z. Säugetierkunde* 35:214-238.
- Kruska, D. (1973) Cerebralisation, Hirnevolution und domestikationsbedingte Hirngrößenänderungen innerhalb der Ordnung Perissodactyla Owen 1848, und ein Vergleich mit der Ordnung Artiodactyla Owen 1848. *Z. Zool. Syst. Evol. Forsch.* 11:81-103.
- Kruska, D. (1988) Mammalian domestication and its effect on brain structure and behavior. In H.J. Jerison and I. Jerison (eds.): *Intelligence and evolutionary biology*. NATO ASI Series, Vol. G17. Springer, Berlin, pp. 211-250.
- Kühlenbeck, H. (1967-1978) *The Central Nervous System of Vertebrates*, 5 vols. Karger, Basel.
- Künzle, H., and G. Rehkämper. (1992) Distribution of cortical neurons projecting to dorsal column nuclear complex and spinal cord in the hedgehog-tentec, *Echinops telfairi*. *Somatosen. Motor Res.* 9:185-197.
- Le Gros Clark, W.E. (1932) The brain of the insectivora. *Proc. Zool. Soc. Lond.* 4:975-1013.
- Lipp, H.P., H. Schwegler, W.E. Crusio, D.P. Wolfer, M.-C. Leisinger-Trigona, B. Heimrich, and P. Driscoll (1989) Using genetically-defined rodent strains for the identification of hippocampal traits relevant for two way avoidance behavior: a non invasive approach. *Experientia* 45:845-859.
- Mann, M.D., S.E. Glickman, and A.L. Towe (1988) Brain/body relations among myomorph rodents. *Brain Behav. Evol.* 31:111-124.
- Mann, M.D., G. Rehkämper, H. Reinke, H.D. Frahm, R. Necker, and E. Nevo. (1997) Size of somatosensory cortex and of somatosensory thalamic nuclei of the naturally blind mole rat, *Spalax ehrenbergi*. *J. Brain Res.* 38:47-59.
- Martin, R.D. (1981) Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature (Lond.)* 293:57-60.
- Martin, R.D. (1990) *Primate Origins and Evolution: A Phylogenetic Reconstruction*. Chapman and Hall, London.
- Martin, R.D. (1995) Hirngröße und menschliche Evolution. *Spektrum Wissenschaft September*, pp. 48-55.
- Meador, D.M., D.M. Rumbaugh, J.L. Pate, and K.A. Bard (1987) Learning, problem solving, cognition, and intelligence. In G. Mitchell, and J. Erwin (eds.): *Behavior, Cognition, and Motivation. Comparative Primate Biology*, Vol. 2, Part B. Liss, New York, pp. 17-83.
- Merzenich, M.M., R.J. Nelson, M.P. Stryker, M.S. Cynader, A. Schoppmann, and J.M. Zook (1984) Somatosensory cortical map changes following digit amputation in adult monkeys. *J. Comp. Neurol.* 224:591-605.
- Nadel, L. (1991) The hippocampus and space revisited. *Hippocampus* 1:221-229.
- Nauta, W.J.H., and H.J. Karten. (1970) A general profile of the vertebrate brain, with sidelights on the anatomy of cerebral cortex. In F.O. Schmitt, (ed.): *The Neurosciences*. Second Study Program, Rockefeller University Press, New York, pp. 7-26.
- Necker, R., G. Rehkämper, and E. Nevo (1992) Cortical representation of the somatosensory system in the blind mole rat, *Spalax ehrenbergi*: an electrophysiological investigation. *Neuroreport* 3:505-508.
- Nevo, E. (1991) Evolutionary theory and processes of active speciation and adaptive radiation in subterranean mole rats, *Spalax ehrenbergi* superspecies, in Israel. *Evol. Biol.* 25:1-125.
- Nottebohm, F. (1981) A brain for all seasons: cyclical anatomical changes in sensory control nuclei of the canary brain. *Science* 214:1368-1370.

- Oboussier, H. (1972) Evolution of the mammalian brain. Some evidence on the phylogeny of the antelope species. *Acta Anat.* 83:70-80.
- Papi, F. (1991) Olfactory navigation. In P. Berthold (ed.): *Orientation in Birds*. Birkhäuser, Basel, pp. 52-85.
- Papi, F. (1995) Recent experiments on pigeon navigation. In E. Alleva, A. Fasolo, H.P. Lipp, L. Nadel, and L. Ricceri, (eds.): *Behavioural Brain Research in Naturalistic and Semi-Naturalistic Settings: Possibilities and Perspectives*. Kluwer, Dordrecht, pp. 225-238.
- Passingham, R.E., and G. Eklinger, (1974) A comparison of cortical functions in man and the other primates. *Int. Rev. Neurobiol.* 16:233-299.
- Paton, J.A., and F. Nottebohm (1984) Neurons generated in the adult brain are recruited into functional circuits. *Science* 225:1046-1048.
- Plögmann, D., and D. Kruška, (1990) Volumetric comparison of auditory structures in the brains of european wild boars (*Sus scrofa*) and domestic pigs (*Sus scrofa f. dom.*) *Brain Behav. Evol.* 35:146-155.
- Rehkämper, G. (1981) Vergleichende Architektonik des Neocortex der Insectivora. *Z. Zool. Syst. Evol. Forsch.* 19:233-263.
- Rehkämper, G. (1997) Zur frühen Rezeption von Darwins Selektionstheorie und deren Folgen für die vergleichende Morphologie heute. *Sudhoffs Arch.* 81:171-192.
- Rehkämper, G., H.D. Frahm, and M. Mann (1995) Brain composition and ecological niches in the wild or under man-made conditions (Domestication). In E. Alleva, et al. (eds.): *Behavioural Brain Research in Naturalistic and Seminaturlistic Settings: Possibilities and Perspectives*. Kluwer, Dordrecht, pp. 83-103.
- Rehkämper, G., H.D. Frahm, and K. Zilles (1991a) Quantitative development of brain and brain structures in birds (Galliformes and Passeriformes) compared to that in mammals (Insectivores and Primates). *Brain, Behav. Evol.* 37:125-143.
- Rehkämper, G., H.D. Frahm, K. Zilles, and E. Nevo (1991b) *Spatax*-Zentralnervöse Anpassungen eines blinden Tieres. Arbeitstagung Würzburg 1990. *Anat. Anz.* 172:67.
- Rehkämper, G., E. Haase, and H.D. Frahm (1988) Allometric comparison of brain weight and brain structure volumes in different breeds of the domestic pigeon, *Columba livia f.d.* (Fantails, Homing pigeons, Strassers). *Brain Behav. Evol.* 31:141-149.
- Rehkämper, G., K.-L. Schuchmann, A. Schleicher, and Zilles, K. (1991c) Enzephalisation in Humming birds (*Trochilidae*). *Brain Behav. Evol.* 37:85-91.
- Rehkämper, G., H. Stephan, and W. Poduschka (1986) The brain of *Geogale aurita* Milne-Edwards and Grandier 1872 (Tenrecidae, Insectivora). *J. Hirnforsch.* 27:391-399.
- Rehkämper, G., and K. Zilles (1991) Parallele evolution in mammalian and avian brains: cytoarchitectonical and cytochemical analysis. *Cell Tissue Res.* 263:3-28.
- Rehkämper, G., K. Zilles, and A. Schleicher (1984) A quantitative approach to cytoarchitectonics. IX. The areal pattern of the hyperstriatum ventrale in the domestic pigeon, *Columba livia f.d.* *Anat. Embryol.* 169:319-327.
- Rehkämper, G., K. Zilles, and A. Schleicher (1985) A quantitative approach to cytoarchitectonics. X. The areal pattern of the neostriatum in the domestic pigeon, *Columba livia f.d.* *Anat. Embryol.* 171:345-355.
- Remme, U. (1962) Über einige statistische Hilfsmittel moderner zoologisch-systematischer Untersuchungen. *Zool. Anz.* 169:93-140.
- Remme, U., and E.E. Weber (1972) An illustration of the principal ideas of MANOVA. *Biometrics* 28:235-238.
- Röhrs, M. (1985a) Cephalisation bei Feliden. *Z. Säugetierkd.* 50:234-240.
- Röhrs, M. (1985b) Cephalization, neocorticalization and the effect of domestication on brains of mammals. In H.R. Duncker, and G. Fleischer (eds.): *Functional Morphology in Vertebrates*. Fischer, Stuttgart, pp. 545-547.
- Röhrs, M. (1986a) Cephalisation, Telencephalisation und Neocorticalisation bei Mustelidae. *Z. Zool. Syst. Evol. Forsch.* 24:157-166.
- Röhrs, M. (1986b) Cephalisation bei Caniden. *Z. Zool. Syst. Evol. Forsch.* 24:300-307.
- Roland, P., and L. Friberg (1985) Localization of cortical areas activated by thinking. *J. Neurophysiol.* 53:1219-1243.
- Roth, G., J. Blankie, and D.B. Wake (1994) Cell size predicts morphological complexity in the brains of frogs and salamanders. *Proc. Natl. Acad. Sci. U.S.A.* 91:4796-4800.
- Ruse, M. (1986) *Taking Darwin Seriously*. Basil Blackwell, Oxford.
- Ruse, M. (1997) *Man to Man. The Concept of Progress in Evolutionary Biology*. Harvard University Press, Cambridge, MA.
- Sauer, E.G.F. (1973) Zum Sozialverhalten der kurzohrigen Elefantenspitzmaus, *Macroscelides proboscideus*. *Z. Säugetierkd.* 38:67-97.
- Schwegler, H., H.-P. Lipp, H. van der Loos, and W. Buschmaier (1981) Individual hippocampal mossy fiber distribution in mice correlates with two way avoidance performance. *Science* 214:817-819.
- Sherry, D.F., L.F. Jacobs, and S.J.C. Gaulin (1992) Spatial memory and adaptive specialization of the hippocampus. *TINS* 15:298-303.
- Shettleworth, S.J. (1990) Spatial memory in food-storing birds. *Philos. Trans. R. Soc. Lond. Biol.* 329:143-151.
- Snell, O. (1892) Die Abhängigkeit des Hirngewichts von dem Körpergewicht und den geistigen Fähigkeiten. *Arch. Psychiat. Nervenkrankh.* 23:436-446.
- Stephan, H. (1960) Methodische Studien über den quantitativen Vergleich architektonischer Struktureinheiten des Gehirns. *Z. Wiss. Zool.* 164:143-172.
- Stephan, H. (1975) Allocortex. In W. Bargmann (ed.): *Handbuch der mikroskopischen Anatomie des Menschen*. Band IV, Teil 9. Springer, Beilines.
- Stephan, H., G. Baron, and H.D. Frahm (1988) Comparative size of brains and brain components. In H.D. Steklis, and J. Erwin (eds.): *Comparative primate biology, vol. 4. Neurosciences*. Liss, New York, pp. 1-38.
- Stephan, H., G. Baron, and H.D. Frahm (1991) *Comparative Brain Research in Mammals, vol. 1, Insectivora* Springer, New York
- Stephan, H., G. Baron, H.D. Frahm, and M. Stephan (1986) Größenvergleiche an Gehirnen und Hirnstrukturen von Säugern. *Z. mikroc. Anat. Forsch. Leipzig* 100:189-212.
- Stephan, H., H.D. Frahm, and G. Baron (1981) New and revised data on volumes of brain structures in insectivores and primates. *Folia Primatol.* 35:1-29.
- Stewart, M., S.P.R. Rose, T.S. King, P.L.A. Gabbott, and R. Bourne (1984) Hemispheric asymmetry of synapses in clitic medial hyperstriatum ventrale following passive avoidance training: a stereological investigation. *Dev. Brain Res.* 12:261-269.
- Stiefken, V. (1993) *Vergleichende Untersuchungen zur Größe von motorischen Zentren in Cerebellum und Hirnstamm der Fledermäuse*. Dissertation, Med. Fakultät, Universität Köln.
- Strube, G. (1996) Kognition. In G. Strube, B. Becker, C. Fiecks, U. Hahn, K. Opwis, and G. Palm (eds.): *Wörterbuch der Kognitionswissenschaft*. Stuttgart, Klett-Cotta, pp. 303-317.
- Towe, A.L., and M.D. Mann (1995) Habitat-related variations in brain and body size in pocket gophers. *J. Brain Res.* 36:195-201.
- Ullinski, P.S. (1983) Dorsal ventricular ridge: a treatise on forebrain organization in reptiles and birds. In R.G. Northcutt (ed.): *Wiley Series in Neurobiology*. John Wiley and Son, New York, pp. 1-265.
- Valverde, F., and L. Lopez-Mascaraque (1981) Neocortical endeavor: basic neuronal organization in the cortex of the hedgehog. 11th Int. Cong. Anat. In *Glial and Neuronal Cell Biology*. Liss, New York, pp. 281-290.
- Veenman, C.L., J.M. Wild, and A. Reiner (1995) Organization of the avian "cortico-striatal" projection system: a retrograde and anterograde pathway tracing study in pigeons. *J. Comp. Neurol.* 354:87-126.
- Wallenberg, A. (1898) Eine Verbindung caudaler Hirnteile der Taube mit dem Striatum. *Neurol. Zentralbl.* 17:300-302.
- Wallenberg, A. (1903) Der Ursprung des Tractus isthmo-striaticus oder bulbo-striaticus der Taube. *Neurol. Zentralbl.* 22:98-101.
- Wilson, B., N.J. Mackintosh, and R.A. Boakes (1985) Transfer of relational rules in matching and oddity learning by pigeons and corvids. *Q. J. Exp. Psychol.* 37B:313-332.
- Zeller, H., and H.J. Karten (1971) The archistriatum of the pigeon: organization of afferent and efferent connections. *Brain Res.* 31:313-326.
- Zilles, K., and G. Rehkämper (1988) The brain of the Orang-utan, *Pongo sabyrius*, with special reference to its telencephalon. In J. Schwartz (ed.): *Biology of the Orang-Utan*. Oxford University Press, New York, pp. 157-176.