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Morphogenetic versus morphofunctional theory: Franz J. Irsigler's intervention in the *Behavioral and Brain Sciences'* discussion on the implications of the "initial brain" concept for brain evolution in Cetacea (1988)

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Introduction, by Mariela Szirko <Mzirko[at]Sion.com>: When in 1987 *Behavioral and Brain Sciences* launched a debate (11, 75-116, 1988) on one of its target articles, hardly could its editors have foreseen that it was to provide a first opportunity for their readers to hear about one of the basic anatomical concepts of the Argentine-German neurobiological tradition. Hardier even could have been for the Argentinian researchers to foresee that such a silence-breaking, first international technical mention in a long time, was to be proferred by a Third-Reich neuroscientist who learned it as a part of a neuroscience later globally eclipsed, perhaps, by its supposed being redolent of horror deeds. Because of this – not of that – I find salutary to briefly remind the episode.

One of the open peer commentaries (p. 95-6) to the *Behavioral and Brain Sciences'* target article was provided by a Prague University's graduate, medical doctor and later race-differences intellectual Professor Franz Johann Irsigler, former senior neurosurgeon at the University in Berlin, and (1939-1945) member of the (then Kaiser-Wilhelm) Institut für Hirnforschung in Berlin-Buch (now Max-Planck-Institut für Hirnforschung in Frankfurt am Main). The institute was directed, 1937-45, by Professor Hugo Spatz (1888-1969), who was also Irsigler's teacher of brain anatomy. On Spatz and the institute during the period of Irsigler's association with them, judgment has been passed: see *e.g*. Benno Müller-Hill, *Tödliche Wissenschaft: Die Aussonderung von Juden, Zigeunern und Geisteskranken 1933-1945* (Hamburg, Rowohlt Verlag, 1984 and many further editions and translations). Commenting on this topic, Katrin Weigmann ("In the name of science. The role of biologists in Nazi atrocities: lessons for today's scientists", *EMBO reports* 2, 10, 871–875, 2001, and refs. therein, in http://www.nature.com/embor/journal/v2/n10/full/embor304.html) points out: "Julius Hallervorden, head of the department of histopathology at the KWI for Brain Research in Berlin-Buch, took the initiative to co-operate with the Euthanasia movement. 'You kill them anyway; at least take out the brains so the material can be used', he said. The brain research community had developed a close network of collaborations between research institutes and psychiatric wards so efficient that the scientists were supplied with an excess of brain material." Prof. Irsigler later (1963) described himself as a student of Spatz also in his later speculative essays on brain evolution. As an adherent to the fallen regime, after 1945 Irsigler left Germany for the Neurochirurgischen Universitätsklinik in Zurich, Switzerland; then, since 1951 and for the rest of his career, he immigrated to South Africa. There he became associated with Pretoria University first, then with the Department of Surgery at the Medical School, Durban; then Paardekraal Hospital, Krugersdorp since about his 1960 participation in the International Congress of Psychiatry, Neurology & Neurosurgery in Washington DC, and coincident contribution, entitled "Allgemeine Operationslehre", to the *Handbuch der Neurochirurgie*, vol. 1, edited by Herbert Olivecrona and Wilhelm Tönnis (Berlin, Springer, 1960). On 25 November 1969, Professor P. V. Tobias, the chairman of the Department of Anatomy at the University of Witwatersrand in Johannesburg, delivered a lecture on "Brain Size, Grey Matter and Race - Fact or Fiction?" in Johannesburg. Irsigler – who describes himself as "somewhat alarmed and grossly disappointed" – was among the audience. Starting a resounding debate, the lecture subsequently (January 1970) became published in the *American Journal of Physical Anthropology* 32; yet before, on 8 December 1969, Irsigler wrote to Tobias to criticize his lecture. Until 1971, Irsigler had published only in the neurosurgical literature; afterward he also emerged as a public critic of racial liberalism (*cf*.

http://www.ferris.edu/isar/bibliography/irsigler.htm). Of all this story, here the point of interest is only what Irsigler's intervention reveals in connection with the reception of Professor Jakob's research results in the German neurobiology after 1911 – and its fate.

This point of interest is Irsigler's having been formed in the 1920' and 1930's in such an intellectual sphere and distinguishing himself in the BBS's debate by pointing out one of Jakob's results, an important technical concept, in 1988. It finely illustrates the sectorization of the results taken into account in doing science and, by the way, it also illustrates the nefarious association of cultures, and the scientific results attained in them, with their political regimes. It probably played a role in the neglect of this relevant technical concept developed decades before in the Argentine-German neurobiological school, of which concept due notice was taken in German neuroscience independently of the tolerance or collaboration of some of its researchers as regards the atrocities perpetrated between 1937 and 1945, and the parallel inattention encountered by this concept in other countries' neurosciences. One cannot help but mind of the cerebral circuit that Jakob described and taught in his lessons since 1907 and he reiterately published since 1909, which another researcher – one, of irreproachable honesty and professional integrity – introduced *bona fide* also in 1937 and is since known as "the circuit of Papez". It, too, illustrates aspects of the dementia dichotoma, *der Zweikulturenwahn* denounced by an earlier collaborator of *Electroneurobiología* (1995: *cf*. http://electroneubio.secyt.gov.ar/Tercero.htm) then President of the Berlin-Brandenburg Academy of Sciences, Prof. Hubert Markl. (Professor Markl was later appointed President of the Max Planck Gessellschaft and set up an important research program to discriminate science and misdeeds at the Kaiser Wilhelm Institut). Irsigler introduced, into the BBS discussion's conceptual landscape, Christfried Jakob's anatomical-developmental concept of hemispheric rotation around the sylvian pivot (*Vom Tierhirn zum Menschenhirn,* 1911), which is the point of interest of the present recounting.

Technical context to Irsigler's commentary: The *Behavioral and Brain Sciences* set up a debate on its target article, "Implications of the 'initial brain' concept for brain evolution in Cetacea" by Ilya I.

Glezer, Myron S. Jacobs and Peter J. Morgane, which became published in *BBS* 11, 75-116 (1988). Open peer commentary was provided, besides Prof. F. Irsigler, by other 24 scientists, seven of whom were from Europe and the remaining from the United States. Glezer, Jacobs and Morgane's abstract was as follows:

"We review the evidence for the concept of the 'initial' or prototype brain. We outline four possible modes of brain evolution suggested by our new findings on the evolutionary status of the dolphin brain. The four modes involve various forms of deviation from and conformity to the hypothesized initial brain type. These include examples of conservative evolution, progressive evolution, and combinations of the two in which features of one or the other become dominant. The four types of neocortical organization in extant mammals may be the result of selective pressures on sensory/motor systems resulting in divergent patterns of brain phylogenesis. A modular 'modification/multiplication' hypothesis is proposed as a mechanism of neocortical evolution in eutherians. Representative models of the initial ancestral group of mammals include not only extant basal Insectivora but also Chiroptera; we have found that dolphins and large whales have also retained many features of the archetypal or initial brain. This group evolved from the initial mammalian stock and returned to the aquatic environment some 50 million years ago. This unique experiment of nature shows the effects of radical changes in environment on brain-body adaptations and specializations. Although the dolphin brain has certain quantitative characteristics of the evolutionary changes seen in the higher terrestrial mammals, it has also retained many of the conservative structural features of the initial brain. Its neocortical organization is accordingly different, largely in a quantitative sense, from that of terrestrial models of the initial brain such as the hedgehog."

In addition, providing an introduction, the three authors added: "We have been studying the morphology of the dolphin brain for many years (see Morgane et al. 1986a; 1986b) and, like earlier investigators (Beauregard 1883; Breathnach 1953; 1960; Kükenthal & Ziehen 1889; Langworthy 1931; 1932), we were struck by the extreme size and convolutional complexity of cetacean neocortical formations. Our histological studies, however, revealed a 'relatively simple underlying neocortical organization in the dolphin that is in many ways similar to that of hedgehogs and bats' (Morgane et al., 1985; 1988 in press). The studies of Sanides (Sanides & Sanides 1972; 1974) and Valverde (Valverde 1983; Valverde & Facal-Valverde 1986; Valverde & López-Mascaraque 1981) on the cortical neuronal structure of the hedgehog and bat provide further evidence of neuroarchitectonic similarities with the neocortex of the dolphin. Our recent studies (Morgane et al. 1985; 1986a; 1986b) have accordingly led us to interpret the dolphin brain in terms of an initial or prototype brain concept that we now propose to elaborate in this target article.

The initial brain concept concerns the evolution of the mammalian nervous system and suggests that the full spectrum of extant patterns of brain organization in mammals arose from a common ancestral mammalian brain (Elliot Smith 1910; Filimonoff 1949; Herrick 1921; Wirz 1950). A number of well-established evolutionary concepts documented by comparative neuromorphology and physiology have been drawn upón in this account. (Ariens Kappers et al. 1936; Brodmann 1909; Ebbesson 1984; Ebner 1969; Elliot Smith 1910; Filimonoff 1949; 1965; Herrick 1921; Kaas 1980; Kesarev 1970; Le Gros Clark 1932; Morgane et al. 1985; 1986a; 1986b; Northcutt 1984; Poliakov 1958; Sanides 1969; 1970; 1971; 1972). The following major features of brain evolution recognized by comparative neuroanatomists will be used in discussing the initial brain concept:

1. There is a general trend toward an allometric increase in the absolute and especially the relative mass of the brain with respect to body size. This implies an increase in the number of functional units (neurons), an increase of interneuronal communication due to the corresponding growth of neuronal processes (dendrites and of the glial channels), leading to tangential cortical growth; (2) a prolonged period of neuronal generation (or a reduction in the number of glial channels), leading to radial increase of the cortex. Both modifications may be caused by the acceleration or retardation of normal developmental processes secondary to DNA changes, in agreement with modern evolutionary views (Gould 1977).

In contrast, changes in the size and shape of cortical neurons may, to some extent, exploit the normal developmental modifiability of neuronal shape, although for more drastic structural and chemical changes in cortical neurons some genetic innovations may be necessary. Normal developmental mechanisms can also allow changes in the number of at least one type of cortical 'module' (Van der Loos & Welker 1985).

Finally, cortical connectivity develops through a phase of initial exuberancy (Innocenti, in press; Innocenti et al. 1977) characterized by the fact that an area or part of an area projects to and receives from a broader and more diverse territory than in the adult, followed by focussing or rededication of these projections. As discussed elsewhere (Innocenti, in press), this developmental strategy might have appeared by fortuitous mutation and then been maintained through phylogenesis because of its adaptive ontogenetic value. Since this strategy may also have allowed the incorporation of genetic caprices such as addition or loss of neurons, the invasion of new territories by a projection, and the segregation of projections into separate territories (Ebbesson 1984; Katz et al. 1983), structures that have adopted this strategy, such as cortex, have enjoyed and still may enjoy explosive evolution." Irsigler's contribution is as follows:

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The target article by Glezer et al. about the "initial brain" concept offers a phylogeny of the cetacean neocortex in terms of its laminar and modular cytoarchitectonics. On that account the Cetacea appear as a unique feature of evolution in the direction of "conservative/progressive" corticalisation. The authors start from an hypothesized archetypal brain model, represented by extant basal Insectivora and Chiroptera. They reconstruct four evolutionary modes by postulating a modification/multiplication model wherein the modular components of the cortical areas are considered to be the elementary functional units and "some of the main targets of evolutionary forces."

In contrast to this, morphogenetic theory starts from extant allocortical (phylogenetically early) formations - that is, reptilian and paleomammalian - preserved throughout vertebrate evolution and considered to be the foundation of species-typical behaviour in man and animal, from the mammal-like reptiles upwards.

Morphogenesis (a well-ordered sequence of transformations) rests on:

1. Allo-isocortical contiguity, that is, "interpenetration" (Edinger 1909) or "interfaces";

2. Hemispheric rotation around the sylvian pivot (Jakob 1911); it involves the sagittal and coronal planes and starts from the peri-insular segment resulting in a maturation gradient (Kahle 1969) which means heterochrony in cortical differentiation;

3. Folding in of the allocortex at the base; there, the allocortex loses contact with the bone (Spatz 1937). These processes are autonomous (Monod 1970) and emerge early in phylogeny and ontogeny (Gegenbaur 1898; Hyman 1962; Kahle 1969; Rose 1935).

4. Different and independent rates and modes of these processes result in lateralisation (dominance) of the two brain halves; that is, in a heterochronic shift of encephalisation.

5. Morphogenesis is closely related to metamorphosis: (a) In both, an orderly sequence of events is involved that cannot be imposed on the evolving system by outside forces; (b) in both, information is transmitted by chemical means, analogous to the mRNA in the Monod-Jacob lactose system. The concept of morphogenetic induction (Spemann 1936) is fundamental in metamorphosis and morphogenesis, uniting both under one heading (Monastra 1986).

6. Chemoaffinity (Sperry 1963) is the essential feature of the reptilian type of brain, which forms the core of the "paracrine" neuraxis and constitutes the "chemoarchitecture" of the brain (Nieuwenhuys 1985); it includes the "R-complex" of MacLean (1978) and the allocortices at the base of the frontal and temporal lobes ("basale Rinde" in the human: Spatz 1937; Jakob 1979).

7. Flechsig's original concept (1920; 1927) of "primary" receptive areas having connections only with adjacent "parasensorv"areas known as "associative areas" was later developed into a "connectivity" (Pribram 1971) hypothesis of neocortical "crossmodal associations" (Geschwind 1965) supposedly underlying the "higher cortical functions in man" (Luria 1980). Contrary to this, it is found that the association cortices belonging to the late-myelinized areas on the Flechsig scale represent the more generalized architectonic pattern (compared to the sensorimotor cortices) and come closest to the general cyto- and myeloarchitectonic scheme of Brodmann (1909) and the Vogts (1919) (Sanides 1970; 1975).

Thus, in the ontogenesis of higher placentals there is a spacetime dislocation between cortices having different rates and modes of differentiation; this results in contiguity of the "primary" areas with paleomammalian and mesocortical (insular) boundary zones (Sanides 1975 and coworkers). According to morphogenetic theory, the crucial feature of this kind of interrelationship is that it is species-typical (innate) and, in the words of Sperry (1983) "largely preorganized independently of sensory input" (p. 95).

Critique of Glezer et al. First, the cortical subdivisions offered in the target article (Figure 5) are artifacts construed to fit a preconceived neocorticalisation scheme. They do not coincide with definite extant mammalian species. Consequently, there is considerable overlap, even with "deviant" Cetacea. Thus, cortical subdivisions based on purely cytoarchitectonic descriptions seem inadequate for speciation and taxonomy. Generally speaking, in the whole cortex there is a definite trend toward progressive differentiation from the paleo- to the eulaminate neocortex (Braak 1980; Brockhaus 1940). Nevertheless, during early development there is a great deal of variability in stratification and myelinization (Humphrey 1966; Kahle 1969; Sanides 170; Stephan 1975), contradicting Glezer's et al.'s emphasis on the uniformity of the vertical modules in different functional types of cortex "extending beyond taxonomic boundaries."

Second, Glezer et al.'s hypothetical mechanism of columnar modification (Figure 7) rests on specific afferent inputs and main efferent layers with intercalated association zones between the primary projection areas (Figure 6). This strongly reminds one of Pavlov's "reflex principle," recently called by Luria (1980) "the modern materialistic psychology" (p. 30). Likewise, Kotchetkova (1960), in studying the specifically human regions in the hominid neocortex, concludes that certain neocortical regions concerned with tool making and praxis ("labour" in the sense of Friedrich Engels), have been the driving forces in anthropogenesis - a view as morphofunctional as that of Glezer at al. (See abstract on Sinanthropus in Edinger 1975, p. 233.)

Glezer et al.'s cytoarchitectonics make the module - a single, variable functional element - the causal determinant, outclassing and superceding all lower levels of neuronal activity; this is not likely to be one of the "main targets of evolutionary forces."

Glezer, Jacobs and Morgane's reply (p. 108) was as follows: "We could hardly agree more with **Irsigler**'s comments about the use of cytoarchitectonic subdivisions for evolutionary generalizations about the neocortex. However, in our case, we are using not only cytoarchitectonic subdivisions of the dolphin neocortex, but also correlations with electrophysiological mappings by Russian authors along with our own Golgi and electron microscopic studies (Glezer et al., in press; Morgane et al., in press). The second point made by Irsigler is evidently based on a misunderstanding. Although vertical cortical modules are accepted as basic components of the morphofunctional organization in the neocortex, there is great variability in the dimensions of the columns as well as in their inner structure. We believe that the quantitative and qualitative variability of columnar organization may reflect functional specializations of different cortical areas. In our view the cortical module is likely to be one of the main targets of evoolutionary forces through the influence of subcortical and peripheral neural mechanisms subjected to selective pressures in specific ecological niches"

(For the complete discussion, details and references, *cf*. the original *Behavioral and Brain Sciences* 11:1, 75-116, 1988).

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