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ONTOGENETIC MECHANISMS OF THE BRAIN SIZE EVOLUTION

J. MLÍKOVSKÝ

Department of Evolutionary Biology, Czechoslovak Academy of Sciences, Praha, Czechoslovakia

The size of any organ is determined in ontogeny by 1) the size of its anlage, 2) its growth rate, and 3) onset and offset, i. e. duration of its growth[1]. Analogically, we may assume that the relative size of any organ (to whole body size) is determined in otogeny by 1) the relative size of its anlage, 2) its relative growth rate, and 3) relative duration of its growth.

This paper will examine the relative role of these parameters in the ontogeny of brain size in vertebrates with a focus on possible changes of the role of these parameters during vertebrate evolution.

Material and Methods

In logarithmic transformation the growth line of brain size vs. body size assumes after a certain initial period of acceleration an approximately linear shape, the slope of which may be interpreted as the relative brain growth rate. The slope of this linear line can be best calculated using the reduced major axis analysis[29]. Two basic approaches are possible: 1) to calculate this slope within species, i.e. using different sized (and different old) individuals of the same species, or 2) to calculate the slope between species, i.e. from brain weight — body weight data on neonates of different species belonging to the same supra-specific taxon. The resulting data are basically the same in both these methods.

I used the „between species" method and reduced major axis analysis in calculating the relative growth rate in birds and mammals. All primary data (brain and body weight in neonates) I extracted from literature. For mammals, the primary source was the compilation of these data by Sacher and Staffeldt[26], which I supplemented by the data on Acomys minous[11], Procyon cancrivorus[12], Mustela vison f. domestica[13], Mustela putorius f. furo[2], and Sorex araneus[34]. On the other hand, I excluded from Sacher and Staffeldt's[26] list all ungulates with birth weight above 10 kg (because of their aberrant position), and Erinaceus europeus and Mesocricetus auratus (because the data on them are apparently incorrect). For birds I used neonatal brain and body weights published by Portmann[21], Pegel'man and Lysov[18] and Sazikova[27]. Full list of all of these data and of references is given in Mlíkovský[16]. Correlations were tested with Bravair's, and regression coefficients were compared using the ANOVA method[31].

The data for the relative growth rate of the brain in poikilotherm vertebrates were all calculated with the "within species" method, and extracted from literature.

Results

In all of the so-called lower vertebrates, i. e. Chodrichthyes[25], Osteichthyes[24], Amphibia[35] and Reptilia[19], both brain and body grow continuously throughout

the animal's life. After a brief initial period (exact duration unknow, but not important in our study), the relative brain growth is linear with a slope of about 0.5 (Table 1), i. e. with a marked negative allometrical trend.

Table 1 — Relative growth rate of brain in selected vertebrate groups. a = slope of the regression line, n = number of species in samples

Taxon	n	a	Ref.
Primates	21	0.979±0.0451	Mlíkovský this paper
Mammalia (excl. Primates)	78	0.865±0.0327	Mlíkovský this paper
Aves	54	0.847±0.0282	Mlíkovský this paper
Sauria	12	0.430	Platel 1974
Urodela	9	0.500	Thireau 1975
Teleostei	8	0.461	Ridet 1973
Selachii	2	0.564	Ridet et al. 1973

From this follows, that in these animals relative brain size is determined in ontogeny only by the relative size of its anlage and its relative growth rate, not by the relative duration of its growth.

Also in birds and mammals (except primates), the relative brain growth starts to be approximately linear after a certain brief initial period, similarly as in above-mentioned lower vertebrates. The slope of relative brain growth in this phase is about 0.85 in both birds and non-primate mammals, i. e. brain grows slightly negatively allometrically. The slope (Table 1) is significantly lower than one in both birds ($F_s = -5.411$, $p < 0.001$) and non-primate mammals ($F_s = -4.126$, $p < 0.001$). However, this linear growth does not proceed life long, but both brain and body cease to grow after some period of life (called usually juvenescence). Moreover, brain always ceases to grow before the body does. This is evidenced in ontogenetic studies on both birds[10, 14, 15, 16, 17, 18, 20, 22, 27, 30, 32, 33] and mammals[2, 4, 5, 6, 11, 12, 13, 28, 34].

Hence, in birds and non-primate mammals, relative brain size is determined in ontogeny by all three possible factors: relative anlage size, relative growth rate, and relative growth duration.

In all primates (both prosimian and simian), brain growth parameters are similar to those in other mammals with the significant exception that the slope of the relative brain growth curve during it linear phase equals one ($a = 0.979 \pm 0.0451$; $F_s = -0.465$, $p > 0.1$; not significantly different from one), i.e. brain grows isometrically with body. This is, in addition to the data on neonates considered here, evidenced also by direct ontogenetic studies on Cercopithecidae[7, 37], Pongidae[3, 7] and Homo sapiens[7, 9]. This means that in primates the brain size is determined in ontogeny solely by its relative anlage size and by relative duration of its growth.

Discussion

That factors of evolution are not invariant in time but evolve is an old idea[36]. However, there has been still no convincing direct evidence for such evolutionary changes of evolutionary factors. The evolution of ontogenetic determination of brain size in vertebrates provides a suitable example (Table 2). The Table 2 shows lucidly that relative anlage size is of importance in all vertebrates, that relative growth rate is of importance in nearly all (incl. ancestral) vertebrates but ceases to be so in Primates, and that relative duration of growth begins to be of importance only in birds and mammals.

Table 2 — Contribution of individual evolutionary factors to the determination of brain size in vertebrate ontogeny

Taxon	Relative anlage size	Relative growth rate	Relative growth duration
Cyclostomata, Chondrichthyes, Osteichthyes Amphibia, Reptilia	yes	yes	no
Aves, Mammalia (excl. Primates)	yes	yes	yes
Primates	yes	no	yes

Moreover, numerical evidence summarized in the Table 1 shows that the relative growth rate of brain increases during evolution in vertebrates, being about 0.4—0.6 in lower vertebrates, about 0.8—0.9 in birds and non-primate mammals, and finally about 1.0 in primates.

Summary

It is generally recognized that both absolute and relative brain size as well as encephalization are of importance for the evolution of psychical abilities of animals (incl. man). All these parameters are established during individual ontogenies. The present paper shows which factors can influence this process and how they change during vertebrate evolution. Three possible factors are recognized: a) relative size of brain anlage, b) relative brain growth rate, and c) relative duration of brain growth to body growth. Changes in the importance of these factors during the vertebrate evolution are observed, being a, b) in lower vertebrates, a, b, c,) in birds and non-primate mammals, and a, c) in primates.

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