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The size of venous foramina and skull capacity in man and selected vertebrate species

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In many experiments it was proved that brain cooling systems in mammals and birds depend on the flow of the cool venous blood into the cranial cavity through a well-developed system of foramina. In order to investigate the anatomical basis of this mechanism a morphological study was undertaken. On 10 species of mammals and birds, a correlation between the skull capacity and the size of its main venous foramina was determined. A computer system of image analysis was used. In man the skull that was the largest, however consisted venous foramina of the smallest size. Moreover, the asymmetry of the foramina and the concentration of the outflow in one dominant foramen was the greatest. Probably the dominance of only one venous foramen on each side of the human skull provides the reduction of flow resistance and creates more advantageous conditions for blood outflow from the skull, and therefore, better conditions for brain cooling. (Folia Morphol 2008; 67: 98–103)

Key words: skull, capacity, foramina, venous outflow, anatomy, vertebrates

INTRODUCTION

Selective brain cooling is a special mechanism of maintaining brain temperature at the level below that of whole body temperature, especially in conditions of hyperthermia [1].

It is obvious that enlargement of the brain in birds and mammals was accompanied by transformations of its vascular system, which role was changed from only yielding of oxygen and eliminating of carbon dioxide into the efficient and specialized cooling system [1–3, 9]. In human evolution these transformations were observed also in fossil hominids [5, 16]. Obviously mechanisms of brain cooling in humans are highly effective however they are not fully understood yet [2, 23–25].

The main way of venous outflow from the human skull is realized by paired and highly asymmetric jugular foramina, in most of the people containing blood from one dominant sigmoid sinus, how-ever this system is very variable [13, 14, 17]. The role of this asymmetry in man and animals was not explained reasonably yet. Thorough morphological and measurement studies on skull venous foramina of man and selected animal species had been performed previously by Wysocki et al. [19–22]. However the size of these foramina has not been previously compared with cranial capacity.

MATERIAL AND METHODS

A total of 100 macerated adult human skulls, 100 skulls of macaques, 80 skulls of hares, 67 skulls of european bisons, 37 skulls of foxes, 25 skulls of mongrel dogs, 22 skulls of cats, 14 skulls of rats, and 11 skulls of African ostriches had been examined. Human skulls represented the 13th century population of the region of Kielce, Poland. Animal skulls were derived from collection of The Main Agricultural Academy, Warsaw, Poland.

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The population studied was equalized upon sex. Gender of each human skull was determined based on obvious gender specific morphological characteristics; however gender of animal skulls was known. The capacity of each skull was measured within 10 cubic centimeters of accuracy by filling the skull with a 2 mm diameter lead shot. The surface area of each venous foramen of the skull was measured from a digital microscope image analysis system utilizing MultiScan. Systematic error was minimized by making three consecutive measurements of each foramina and calculating the mean (average) values, however the error was calculated as being about 10% (calculating it by measuring a surface of figure of known area).

The data analysis was performed with several statistical methods. The Student's T-test and Analysis of Variance (ANOVA) (with F-Snedecor distribution) were used to analyze differences between the foramina with two main factors (gender and side). The Test for Pair Dependent was utilized in analysis of the right and left variation of paired foramina. The Pearson test was used to calculate the correlations. The Step Regression Model of Efroymson was used for the regression analysis. A p value of 0.05 was considered as statistically significant.

RESULTS

A pair of foramina, which were the largest and were responsible for the direct flow into the internal or external jugular veins were acknowledged as main venous foramina of the skull. In the majority of mammals they were consistent with jugular foramina, however in bison there were postglenoid foramina, and in ostrich — the so-called venous foramina, situated in close vicinity of the foramina of the 10th cranial nerve.

The foramina were always characterized by smaller or greater asymmetry in favour of one body side. Therefore it was possible to indicate a larger foramen (V) and a smaller one (v) from each pair. Similarly, for all the venous foramina of the skull on each body side the total area of foramina of the dominant side (S) and the total area of the opposite side (s) were calculated. A share of the area of the main pair of foramina, the larger and smaller ones (V + v) in the total area of all the venous foramina of the skull (S + s) depicts the level of concentration of the venous outflow in one, dominant pair of foramina in certain species. It has been presented in the column I in Table 1 and on diagram (Fig. 1).

Columns II and III in Table 1 and on diagram (Fig. 2) however, depict the level of disproportion in the size of the foramina on each side. The coefficient of the disproportion between the main foramina (V/v) was calculated by dividing the area of the main larger foramen (V) by the area of the main smaller foramen (v). On the other hand, the asymmetry of all the skull foramina was calculated per side where first, the whole area of all the added foramina was calculated for each side and then the dominant side was established.

The number and the size of the foramina that "accommodate" the skull of a certain capacity in humans and animals is depicted in a simplified manner by the radio index of the sum of the surface of both the main viscous foramina of the skull, the larger one and the smaller one (V + v/C) and the skull capacity C (S + s/C). These data have been presented in the two last columns in Table 1 and in diagram (Fig. 3).

Among the data that have been presented in Table 1, the statistically important differences regarded the particular values of the size parameters derived on human subjects and animals, and compared in pairs: human and particular animal species as well as all the animals together in comparison to the man (Fig. 4). On the other hand, the differences between the particular species of animals were too unstable and did not form any logical conclusion.

In man, the parameter that had the closest correlation with the skull capacity is the sum of the areas of both jugular foramina (V + v) and the V/v index. In animals, it was only in the case of macaque and ostrich that the areas of both main venous foramina had the strongest correlation with the skull capacity.

DISCUSSION

The gathered results allow for making a claim that the efficient brain cooling system has been created by a number of elements. Centralization and asymmetry of the system of the blood outflow has been established through a reduction of the number of the venous foramina of the skull and development of the pair of two main jugular foramina where of thereof is usually dominant. This leads to the reduction of the flow resistance and the decrease of turbulences [12]. Therefore, relatively small jugular foramina of the human skull operate the skull of considerable capacity, while in animals, large and multiple venous foramina operate smaller skull capacity, which is excellently illustrated by the diagram in Figure 4. Additionally, from the point of view of physics, the upright position of the body in the

Table 1. Parameters calculated on the base of the measured areas of skull foramina with standard deviations (in parentheses) and ranging below. All the parameters are relative and present ratios between two values: greater one and smaller one, so there are no denominations. Description of symbols used in Table was previously given in text, however it is also put below

Species/parameter	V + v/S + s	V/v	S/s	V + v/C	S + s/C
Human	0.59 (0.1)	1.62 (0.55)	1.41 (0.37)	0.08 (0.02)	0.14 (0.03)
	0.35–0.84	1.0–3.47	1.0–2.77	0.03–0.147	0.03–0.25
Macaque	0.43 (0.11)	1.23 (0.23)	1.11 (0.1)	0.17 (0.06)	0.31 (0.09)
	0.22–0.67	1.0–2.34	1.0–1.45	0.05–0.36	0.12–0.6
Bison	0.26 (0.04)	1.42 (0.41)	1.12 (0.12)	0.22 (0.05)	0.87 (0.14)
	0.18–0.33	1.01–2.87	1.0–1.56	0.14–0.34	0.63–1.19
Fox	0.45 (0.06)	1.11 (0.1)	1.09 (0.07)	0.37 (0.04)	0.82 (0.07)
	0.36–0.59	1.0–1.46	1.0–1.29	0.30–0.45	0.68–1.0
Dog	0.4 (0.05)	1.12 (0.12)	1.13 (0.12)	0.36 (0.09)	0.92 (0.21)
	0.28–0.49	1.0–1.37	1.0–1.56	0.22–0.6	0.57–1.35
Cat	0.16 (0.04)	1.27 (0.24)	1.15 (0.16)	0.27 (0.09)	0.67 (0.16)
	0.09–0.27	1.0–1.88	1.02–1.69	0.13–0.54	0.44–1.0
Hare	0.44 (0.1)	1.36 (0.42)	1.22 (0.19)	0.34 (0.11)	0.82 (0.19)
	0.23–0.71	1.0–3.85	0.86–1.97	0.14–0.70	0.42–1.41
Rat	0.23 (0.09)	1.33 (0.26)	1.11 (0.1)	0.78 (0.14)	3.3 (0.58)
	0.16–0.43	1.01–1.78	1.01–1.36	0.56–0.94	2.7–4.85
Ostrich	0.39 (0.12)	1.25 (0.19)	1.19 (0.12)	0.16 (0.05)	0.61 (0.13)
	0.22–0.61	1.0–1.61	1.01–1.36	0.12–0.30	0.35–0.8

V — area of greater main venous foramen of the skull; v — area of smaller main venous foramen of the skull; S — sum of areas of all venous foramina of the skull of the dominant side; s — of areas of all venous foramina of the skull of the non-dominant; C — capacity of cranial activity
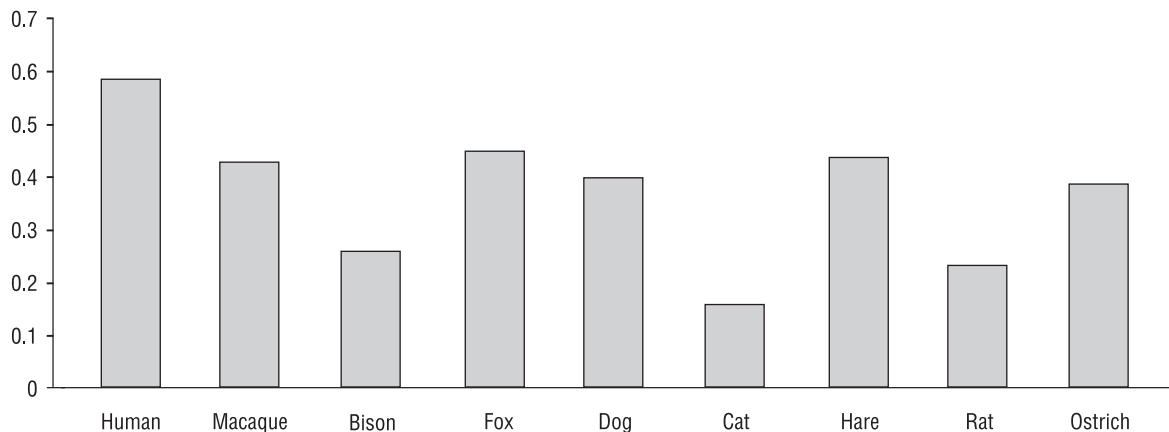

Figure 1. Comparison of participation of jugular foramina of both sides (V + v) in total area (S + s) of skull venous foramina in particular animal species.

process of hominization probably created advantageous conditions to the venous outflow by adding the force of gravity to other forces which facilitated outflow of venous blood.

Significant and even dramatic changes of pattern of the venous system inside the cranial cavity were really visible in early hominids, which were maybe connected with bipedality [5, 16, 18]. Bipedality established as a manner of locomotion about 4 million years ago in Australopithecus [8]. The upright position had made hands disengaged, enlarged content of visual information incoming to the brain
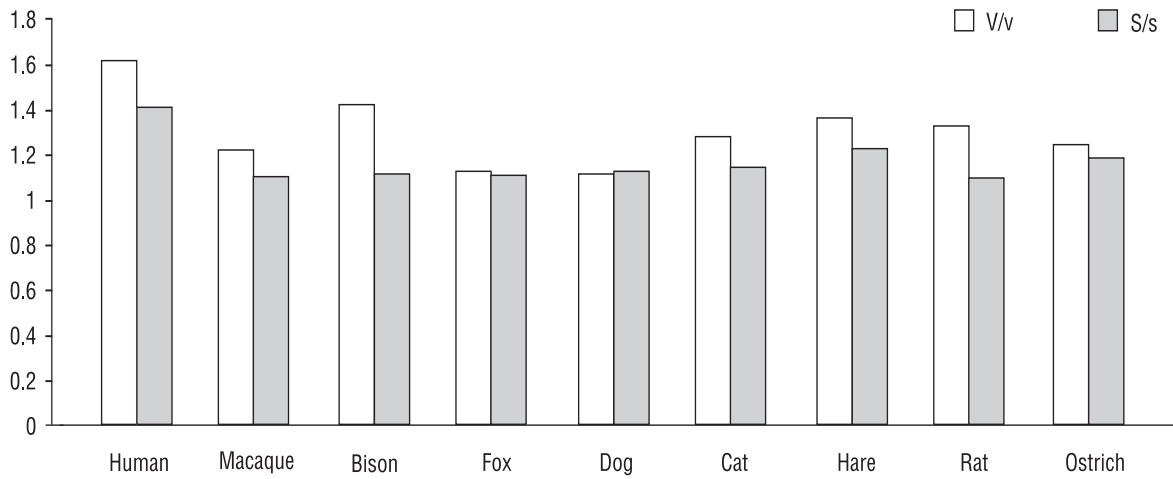
Figure 2. Comparison of asymmetry of areas of jugular foramina or their analogues (V/v) and asymmetry of sum of all skull venous foramina (S/s) regarding skull side in particular animal species.
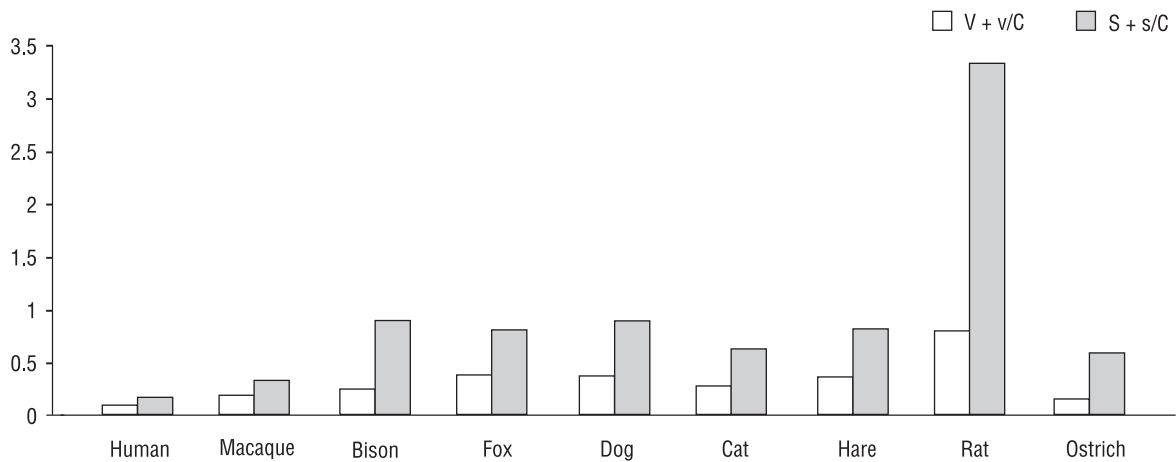

Figure 3. Comparison of the ratio of area of studied skull venous foramina to skull capacity (V + v/C and S + s/C) in particular animal species.

and created better conditions for venous outflow from the skull, adding to the other forces also force of gravitation [4–6, 15]. The results of physiological experiments on humans, according to which changing body position from horizontal to vertical considerably decreases transtympanal temperature, indirectly confirm this thesis [10].

Some new physiological regulatory mechanisms allowed early hominids to live on very dry and warm East-African savanna as for the heat excess appears as the greatest problem in such climatic conditions [8]. In evolution of hominids one can observe interesting changes in morphology of venous sinuses of dura mater, which could be possible to read off on the base of their grooves on the skull vault and base.
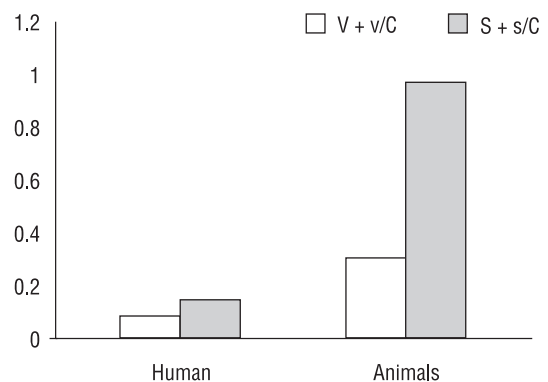

Figure 4. Comparison of indexes: V + v/C and S + s/C for humans and all the animals separately.

In the first stage of these evolutionary changes the main stream of blood outflow from the brain was directed to vertebral plexus through the foramen magnum, according to gravitation force direction and using just existing venous anastomoses [5]. Subsequently another change, resulting in transition from the occipital/marginal sinus domination model to transverse/sigmoid sinuses model with a favorable position of jugular foramina could be observed [5, 16]. Weightiness of skull venous foramina situated above the jugular ones subsequently diminished [16]. Characteristic orientation of the superior sagittal sinus tributaries (contrastream) also appears in the hominization process very late and it is absent in other mammals [11]. In Australopithecus robustus, Australopithecus boisei and Australopithecus afarensis system of occipital/marginal sinuses dominates, however in Australopithecus africanus a specific dual pattern exists, based upon both occipital/marginal and transverse/sigmoid systems been well developed [16]. In these species there was also observed right side domination, especially considering lateral sinuses. During these transformations developed also smaller, additional ways of venous outflow, which are either absent or weak in other primates, as: multiple hypoglossal canals, condylar canal, mastoid, parietal and occipital emissaries [5]. In the transient stage they became important accessory routes [5, 7]. Nowadays in contemporary man, where the transverse/sigmoid sinuses dominate, these additional routes of venous outflow seem to be of minor importance [14]. Moreover, it became the necessity to develop a special system to regulate the direction and the size of the flow between the interior of the skull and its surface [24, 25].

CONCLUSION

1. Parameters quantifying ratio of skull venous foramina to skull capacity present important interspecies differences majority of the studied species.
2. Ratio of area of skull venous foramina to the skull capacity is in man considerably lower than in all investigated animal species.
3. Assymmetry of the main venous foramina of the skull is in close correlation with skull capacity only in man and macaque.
4. In cases of extreme asymmetry of jugular foramina in man the ligation of jugular vein, especially on the dominant side, should be dissuaded.
5. In human there is the greatest concentration of the skull venous drainage expressed with preponderance of one of jugular foramina.

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