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Extension of the "Membranes as Metabolic Pacemakers" Theory to Fowl Species and their Metabolically Active Tissues

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Biological membranes, made-up basically by Phospholipid (PL) bilayers are the basis of cellular organization. In 2007 Hulbert et al. [1] reviewed the mechanism underlying their regulatory role; in particular how membrane integrated Fatty Acyl (FA) chains modify Basal Metabolic Rate (BMR). On a cellular level BMR involves synthetic processes and the maintenance of trans-membrane ion gradients [2,3]. The molecular activity of transmembrane (e.g. Na^+/K^+ ATPase) enzymes is likewise determined or markedly influenced by the physico-chemical properties of the surrounding membrane lipids, thus, membranes have postulated to act as "pacemakers of the metabolism" [4]. As body mass and BMR are allometrically related [5], membrane fatty acyl chain composition and body mass are also related allometrically in homeothermic species [6].

In mammals some metabolically active tissues (heart and skeletal muscle, liver, kidney) were found to provide defined allometric scaling of their membrane FA chains. With the exclusion of the brain, tissue phospholipids of differently sized mammals provide negative allometry for the unsaturation index (number of double bonds in 100 FA chains), the total n3 FAs and the docosahexaenoic acid proportion [1]. In contrast, the level of monounsaturation has been found to be positively related to body mass, as well as the level of total n6 fatty acids.

In birds *pectoralis* [7] and heart muscles [8] were first subjected to allometric PL FA analysis, providing characteristic, body mass related variations. Moreover, sub-cellular fractions [9] and organelles [10] have been studied in birds, from which all but the brain microsomal PL FAs have been found to be allometrically related to body mass. The characteristics of these relationships were analogous with those found in the mammals. In 2010 our results [11] on splanchnic avian organs (total lung, kidney and liver) showed that the phospholipid fatty acyl chain composition is far not random, but follows the membranes as metabolic pacemakers theory in a quail - turkey (150 g - 20 kg) body mass spectrum, with the very determinant contribution of Docosahexaenoic Acid (C22:6 n3, DHA). In 2012 a further intriguing question arose: if the avian, tubularly structured lung *in toto* provides allometric allocation of the total PL FA composition, which lipid compartment is determining this relationship? We thus separately analysed the thoroughly lavaged avian lung (parenchyma) and the phospholipidous lining film, the avian surfactant. Interestingly, both fractions provided negative allometric scaling for DHA, albeit the contribution to the overall results of surfactant was minor [12]. The interesting point of this finding was that DHA in surfactant plays a minor role, mainly modifying the adhesion of secreted surfactant to the cellular surface. It seems thus that intracellular, not exocytozed surfactants (lamellar bodies) are also composed according to a metabolic rate dependent manner, which can be still detected in the secreted moiety.

Very interestingly, avian cerebral total PL FA composition fails to provide allometric regularities. Most probably the reason of this phenomenon is that brain adapts to the increased metabolic needs with a volumetric adaptation, while other metabolically active organs provide increased mass dependent metabolic rate (i.e. O_2 consumption/g). Another limitation of the metabolic pacemaker theory was found when analysing turkey *pectoralis* muscle membrane lipids in a wide body mass range during ontogenesis [13]. In this case the single sided selection for muscle production or the minor metabolic rate alteration of skeletal muscle may have been the conditions making the above-cited theory not valid.

Based on the concept that the rate of *in vivo* lipid peroxidation is strongly modified by the level of fatty acid unsaturation, in all above mentioned studies the whole organ malondialdehyde level was as well determined, mostly to ascertain whether lipid peroxidation also follows allometric patterns. This has been indeed proven in the avian heart, kidney liver and lung, with different allometric exponents, but with statistical significance.

Summarized, it seems that the membranes as metabolic pacemakers theory applies for most of the metabolically active avian organs, with the exception of the brain, and DHA plays a crucial role in this process. Since lipid peroxidation is exponentially augmented with the increase of the number of unsaturated bonds in the fatty acyl chains a cytotoxic end product, malondialdehyde was found also to provide body mass related concentrations. Thus, our results added a confirmatory part to the rate of living theory in an avian cohort, *Galliformes*, which are characterized with short maximal lifespan and expressed lipid peroxidation rates.

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