Alma Dzib-Goodin   [1]
Daniel Yelizarov   [2]

Evolution of movement process as a key for human cognition.

Evolución del movimiento como clave para la cognición humana.

Evolução do processo de movimento como uma chave para a cognição humana.

[1]   Learning & Neuro-development Research Center, Address: 6450 Cape Cod Ct Lisle, Illinois 60532. USA. ORCID: 0000-0001-9705-9153

[2]   Learning & Neuro-development Research Center, Address: 6450 Cape Cod Ct Lisle, Illinois 60532. USA. ORCID: 0000-0002-1960-4811

Contacto: Alma Dzib-Goodin: Postal address: 12 Becker St. Port Towsend, WA. 98368 USA. E-Mail: alma@almadzib.com

ABSTRACT

Movement is defined as a complex event in both the evolution of species and human development, which involves genetic and epigenetic mechanisms. It is linked with memory, attentional and linguistic processes, and it is required to create and use tools, defined as an extension and externalization of human hands, or the motor organs or effectors, so we believe is the basis of human cognition. The process created a parietal plasticity when incorporating tools into the body schema, which gave place to brain expansion by tool-use training. This sequence is considered relevant to the Homo sapiens development, and produces such level of sophistication to every cultural expression, that makes movement an important process both phylogenetic and ontogenetically.

Under this context, this article covers the evolution of movement as a process. It begins with the first molecular actions to create a mechanism to retain energy and metabolize food. Additionally, this article explains: 1) how motility opened a door to the evolution of species, 2) how actin gets an important role in the cytoskeletal support, and 3) the development of the skills that allowed them to survive. Lastly, we investigate the evolution of movement as an adaptation to the environment, and the design of a human brain capable of pushing not only every muscle to the limit, but becoming part of other systems as memory, language or attention, as part of the cognitive processes on humans.

Keywords: Movement; evolution; actin proteins; cell evolution; Central Nervous System development; cognition; Memory; Language.

RESUMEN

El movimiento, desde la perspectiva evolutiva, es una necesidad de las especies para sobrevivir sobre la faz de la tierra, que involucra mecanismos tanto genéticos como epigenéticos, vinculados a los procesos de memoria, atención y lenguaje, necesarios para crear y usar herramientas, empleadas como extensión de las manos humanas y de los órganos motores o efectores. Esto creó una plasticidad parietal al incorporar herramientas en el esquema del cuerpo, y dio lugar a la expansión del cerebro mediante el uso de las mismas y el aprendizaje de cómo usarlas. Esta secuencia se considera relevante para el desarrollo del Homo sapiens, y convierte al movimiento en un proceso filogenética y ontogenéticamente importante.

En este contexto, este artículo cubre la evolución del movimiento como proceso. Comenzando con las primeras acciones moleculares para crear un mecanismo capaz de retener la energía y metabolizar los alimentos. Además, este artículo explica: 1) cómo la motilidad abrió una puerta a la evolución de las especies, 2) el papel de la actina en el apoyo al cito esqueleto, y 3) el desarrollo de habilidades que permitieron la pervivencia de las especies. Por último, se investiga la evolución del movimiento como adaptación al medio ambiente, y el diseño de un cerebro humano capaz de empujar no sólo cada músculo al límite, sino convertirlo en parte de otros sistemas como la memoria, el lenguaje o la atención, como parte del proceso cognitivo en los seres humanos.

Palabras clave: Movimiento; Evolución; Proteína actina; Evolución celular; Desarrollo del Sistema nervioso central; Cognición; Memoria; Lenguaje.

RESUMO

O movimento, de uma perspectiva evolutiva, é uma necessidade da sobrevivência das espécies na face da terra, que envolve mecanismos genéticos e epigenéticos, ligados aos processos de memória, atenção e linguagem, necessários para criar e usar ferramentas, usadas como uma extensão das mãos humanas e dos órgãos motores ou efetores. Isso criou uma plasticidade parietal incorporando ferramentas no esquema do corpo e resultando na expansão do cérebro através do uso do mesmo e aprendendo a usá-las. Esta sequência é considerada relevante para o desenvolvimento do Homo sapiens e torna o movimento um processo filogenético e ontogenético importante.
Neste contexto, este artigo aborda a evolução do movimento como um processo. Começando com as primeiras ações moleculares para criar um mecanismo capaz de reter energia e metabolizar alimentos. Além disso, este artigo explica: 1) como a motilidade abriu uma porta para a evolução das espécies, 2) o papel da actina no apoio ao citoesqueleto e 3) o desenvolvimento de habilidades que permitiram a sobrevivência das espécies. Finalmente, investigamos a evolução do movimento como uma adaptação ao meio ambiente e o design de um cérebro humano capaz de levar não apenas cada músculo até ao limite, mas convertê-lo em outros sistemas, como memória, linguagem ou atenção, como, por exemplo, parte do processo cognitivo em seres humanos.

Palavras-chave: Movimento; Evolução; Proteína Actina; Evolução celular; Desenvolvimento do sistema nervoso central; Cognição; Memória; Linguagem.

ORIGINALES / ORIGINAL PAPERS

"Nature is ever at work building and pulling down, creating and destroying, keeping everything whirling and flowing, allowing no rest but in rhythmical motion, chasing everything in endless song out of one beautiful form into another"

John Muir

Cell movement can be a physical, chemical, diffusible or non-diffusible signal that is detected by receptor proteins located on the cell membrane, and transmitted by them via signaling cascades to the cell interior (Ananthakrishnan and Ehrlicher, 2007).

This process is possible thanks to a very complex network of genes, proteins, and enzymes but involves a constant restructuring of the actin cytoskeleton, through the following three stages in most cells. First, a cell propels the membrane forward by orienting and reorganizing (growing) the actin network at its leading edge. Second, it adheres to the substrate at the leading edge and deadheres (releases) at the cell body and rear of the cell. Third, contractile forces, generated largely by the action of the acto-myosin network, pull the cell forward (Ananthakrishnan and Ehrlicher, 2007).

However, this feature didn't begin from one day to another. At some early point of life in the earth, it required the introduction of ATP as the universal energy, which was an important step in bioenergetic evolution, displacing acetyl phosphate (Sousa, Thiergart, Landan, Nelson-Sathi, Pereira, Allen, Lane, and Martin, 2013). However, even if ATP is universal across ancestries, it is not the sole energy within the metabolism of individual cells in early biochemistry, it needed time to become so important. The most accepted explanation for ATP's rise to prominence is that it was a consequence of the substrate specificity of the rotor stator-type ATPase. This protein, which is as universal among cells as the code (Thauer, Kaster, Seedorf, Buckel & Hedderich, 2008) of all biological energy in the form of ATP, comes ultimately from chemiosmotic coupling the process of charge separation from the inside of the cell to the outside, and the harnessing of that electrochemical gradient via a coupling factor, an ATPase of the rotor–stator-type (Martínez-Cano, Reyes-Prieto, Martínez-Romero, Partida-Martínez, Latorre, Moya, and Delaye, 2015).

All of these mechanisms were drafted long before the modern eukaryote cell. Prokaryotes, the first living organisms, developed in a protected and chemically rich medium, with different ways to get energy in order to move. Protein kinasa cyclic nucleotide-binding (CNB) domains are widespread in the prokaryotic world. They appear to be an ancient motif that has co-evolved with the adenylyl cyclase pathway or cAMP as a mechanism for translating the stress-induced cAMP second messenger into a biological response. Both cAMP and cGMP domains are first found functionally linked to an EPK early in the evolution of eukaryotes, so they are found, for example, in all fungi (Taylor, Keshwani, Steichen, and Kornev, 2012).

Beside, motility required the integration of nuclear and other cellular functions as a bidirectional transport across the nuclear envelope. As translation is cytoplasmic since this requires that all tRNA, rRNA and mRNAs must be exported, while proteins required for DNA replication, transcription, transcriptional regulation, RNA processing and overall nuclear organization are imported (Wickstead and Gull, 2011; Koumandou, Wickstead, Ginger, van der Glezen, Dacks and Field, 2013; Blombach, Smollet, Grohmann, Werner, 2016).

Motility: from Prokaryotes to Eukaryotes

There is not a consensus about how the first cells began, however accumulating data suggest that the eukaryotic cell originated from a merger of two prokaryotes, an archaeal host and a bacterial endosymbiont, but, since prokaryotes are unable to perform phagocytosis, the predator had to be a small (facultative) aerobic α-proteobacterium, which penetrated and replicated within the host periplasm, and later became the mitochondria. This created an interaction that took place and may have led to the contemporary complex eukaryotic cell (Davidov & Jurkevitch, 2009).

Once this machinery was in place, the primitive eukaryote could become a predator with the ability to engulf bacteria and archaea. Much of this engulfment would have been for food, but eventually endosymbiosis would lead to the development of a mitochondria and chloroplasts; but two developments would be important to

achieve phagocytosis. First, the organism would have to lose its rigid cell wall, leaving a flexible plasma membrane that could be modulated to project and surround prey.

Second, the organism would need a mechanism for projecting the membrane in a manner that could engulf prey. This would require a cytoskeleton that could produce localized forces. The eukaryotic actin cytoskeleton can generate force on the membrane by two mechanisms: a) a protrusion force generated by the simple act of polymerization and b) a motor molecules to slide the actin filaments relative to each other or to a membrane (Cox, Foster, Hirt, Harris, and Embley, 2008).

If this happened, then the polymerization-based membrane protrusion mechanism would have developed naturally as a result of actin assembly, while the addition of contractile mechanisms involved many steps to evolve the set of motor molecules and actin-binding proteins (Wickstead and Gull, 2011). The problem with this idea is that some archaea and mollicutes have no cell wall and already meet this requirement (Cavalier-Smith, 2002).

In this sense, eukaryotic actin-based have microfilaments and tubulin- based microtubules, and several of the filaments of the bacterial cytoskeleton are intrinsically "cytomotive". This means that the laments themselves can act as linear motors driven by the kinetics of polymerization/depolymerization. Some researchers have explained that In eukaryotes, this activity has been hugely augmented by the evolution of multiple classes of motors, as well as a menagerie of nucleators, severing agents, tip-binding factors, and (de) polymerases. Other cytoskeletal laments appear to be more structural in function, providing resistance to external force or acting as a scaffold (Wickstead and Gull, 2011).

Another hypothesis is called the neomuran hypothesis, which tries to explain the origin of archaebacteria and its diversification. Cavalier-Smith (2002) explains it this way: "Archaebacteria originated by two successive revolutions in cell biology: a neomuran phase shared with their eukaryote sisters followed shortly by a uniquely archaebacterial one. The first, neomuran phase was

an adaptation to thermophily and involved a really major transformation of 19 key characters, including replacement of the cell wall peptidoglycan murein by N-linked glycoprotein and a great upheaval in the cell's protein-secretion and DNA-handling machinery. The second, relatively minor phase of specifically archaebacterial innovations, notably replacement of acyl ester membrane by isoprenoid tetraether lipids and of eubacterial flagellin by glycoproteins, involved further adaptations to hyperthermophily and hyperacidity, respectively. Substantially later, several lineages independently readapted secondarily to mesophily. Lateral transfer of genes from the immensely older and far more diverse eubacteria often played a role in these secondary returns to mesophily and may also have done in the origins of archaebacterial hyperthermophily, sulphate reduction by Archaeoglobus and methano-genesis. Under this perspective, the origin of the first eubacterial cell could be 3700 millions of years ago, with peptidoglycan walls and photo- synthesis, and the origin about 850 My ago of the ancestral neomuran cell, when N-linked glycoproteins replaced peptidoglycan and the pre-eukaryote neomurans evolved phagotrophy, internal skeletons and the endomembrane system" (Cavalier-Smith, 2002).

Another ingredient to allow motility in cells is the structural and architectural properties of the cytoskeleton. The cytoskeleton is comprised of three polymer systems: actin filaments (Wickstead and Gull, 2011) microtubules, and intermediate filaments. Actin filaments form long, thin fibers. These are about 8 mm in diameter and, being the thinnest of the cytoskeletal filaments, are also called microfilaments. Microtubules, participate in a wide variety of cell activities, they are protein motors that use the energy of ATP to provide the motion. Finally, the contribution of intermediate filaments is small and dependents on substrate stiffness and indentation depth and intermediate filaments their principal function is structural (Lodish, Berk, Zipursky, et al., 2000), to reinforce cells and to organize cells into tissues and epidermal cells, which

are composed largely of proteins (Jalilian, Heu, Cheng, Freittag, Desouza, Stehn, Bryce, Whan, Hardeman, Faith, Schevzov, Gunning, 2015).

Actin protein and its role in the cytoskeletal support

The actin cytoskeleton is regulated by a plethora of actin binding proteins and specific signaling pathways. It is also regulated by a complex array of over 15 different types of actin filament structures which have been identified in metazoans that can change in both spatial and temporal intracellular distribution in response to physical and environmental stimuli (Lodish, Berk, Zipursky, et al. 2000).

Two filament-forming protein families, tubulin and actin 7, dominate the cytoskeletons of all extant eukaryotes. Actin filaments are semi flexible polymers with Lp ~17 μm. They are ~7 nm in diameter, are built from dimer pairs of globular actin monomers, and are polar functionally in nature. This means that they have a fast and slow growing distinct end (called the plus end and minus end respectively). The minus end has a critical actin monomer concentration that is ~6 times higher than that at the plus end (~0.6 μM and ~0.1 μM at the minus and plus end respectively). When the end of an actin filament is exposed to a concentration of monomeric actin that is above its critical concentration, the filament end binds monomers and grows by polymerization (Satir, 2016; Lodish, Berk, Zipursky, et al. 2000).

Conversely, when the concentration is below the critical concentration, monomers detach from the filament end, and the filament shrinks by depolymerization. Simply by having these two different critical actin concentrations at the opposing ends of the filament, actin filaments can grow asymmetrically, and when the actin monomer concentration lies between the two values, only the plus end grows while the minus end shrinks. This process, where the length of the filament stays roughly constant and the polymerized monomers within the actin filament transfer momentum forward due to asymmetric plus end polymerization, is known as tread milling, and this is a critical aspect of how polymerizing actin filaments can generate force (Medina, Worthen, Forsberg, Brenman, 2008).

On the other hand, microtubules are the stiffest of the biopolymers, with Lp ranging from 100 to 5000 μm depending on the filament length, (Hightower and Meagher, 1986), and act as helices that may be tightly packed into bundles where all the helices are aligned and this is critical to movement (Satir, 2016).

Actin is a globular major component of the cellular cytoskeleton and one of the most abundant cellular proteins (Jalilian, Heu, Cheng, Freittag, Desouza, Stehn, Bryce, Whan, Hardeman, Faith, Schevzov, Gunning, 2015), and the most highly conserved eukaryotic protein (Satir, 2016) found from unicellular organism to plants, animals, (Siccardi and Adamatzky, 2016; Medina, Worthen, Forsberg, Brenman, 2008; Hightower and Meagher, 1986) and fungi (Roy-Zukav, Dyer, Meagher, 2015).

Approximately 60 actin-binding proteins have been characterized in animals and participates in many essential cellular processes, such as cytoskeletal structure, maintenance of cell shape, cell motility, cell division, endocytosis and intracellular transport, (Guljamow, Delissen, Baumann, Thünemann, Dittmann, 2012) vesicle and organelle movements, cytokinesis, muscle contraction, (Goodson and Hawse, 2002) modulation of a variety of membrane responses, translation of several mRNA species, and modulation of enzyme activity and localization within the cell (Monshausen and Haswell, 2013).

Actin is a member of a larger superfamily of proteins, (Thomas and Staiger, 2014) which acts as a highway connecting different points of the cell and utilizing molecular motors powered by filament assembly forces to transport proteins and organelles across the cell's span (Yi, Huang, Yang, Lin, Song, 2016). As addition it has a signature feature, the polymerization into filaments, is the basis for a remarkable functional versatility and the resultant extensive prevalence of actins in the living world (Bertola, Ott, Griepsma, Vonk and Bagowki, 2008).

However actin must be exquisitely regulated during cell migration, cell adhesion, cell division, and many other essential cellular functions, because actin also forms the core of many cellular structures including filopodia, lamellipodia, microvilli and stress fibers (Zhu, Zhang, Hu, Wen and Wang, 2013).

Actin exists predominantly in one of two forms: monomeric actin (G-actin) and filamentous actin (F-actin). The inter-conversion between these two actin forms is tightly regulated by a diverse array of proteins that bind actin directly or indirectly. Actin depolymerizing factor (ADF), also known as Cofilin, represents one actin-binding protein that can disassemble actin by severing and depolymerizing actin filaments (Bertola, Ott, Griepsma, Vonk, and Bagowki, 2008; Van den Ent, Amos, Löwe, 2001).

While the actin-depolymerizing factor/cofilin (ADF/CFL) gene family proteins have been implicated in cellular processes that range from membrane and lipid metabolism to mitochondrial dependent apoptosis. The tissue, and temporal-specific partitioning of expression patterns suggests that ADF/CFL protein variants have sub-functionalized, but also may have gained novel functions during their evolutionary history. Mammalian CFL and ADF/Destrin have biochemical differences that are highly suggestive of functional divergence (Roy-Zukav, Dyer, Meagher, 2015).

Such level of control is possible thanks to network architecture. Eukaryotes employ more than 100 actin binding proteins (ABPs) generally falling in two classes with either actin monomer or filament binding properties. The numerous interactions of ABPs with actin are believed to be responsible for the evolutionary constraint on its sequence, making it one of the most conserved proteins (Van den Ent, Amos, Löwe, 2001). Except for conventional actin, eukaryotic cells also contain actin-like (ALPs) and actin-related proteins (ARPs), which have well-characterized roles in cytoskeletal functions (Venticinque, Jamieson, Meruelo, 2011).

Six primary actin isoforms have been identified in higher vertebrates, (Goodson and Hawse, 2002) and arthropods, (Brunet and Arendt, 2016; Monshausena and Haswell, 2013). being alpha-skeletal (ACTA1), alpha-cardiac (ACTC1), alpha-smooth muscle (ACTA2), gamma smooth muscle (ACTG2), beta-cytoplasmic (ACTB) and gamma-cytoplasmic isoactin (ACTG1). Moreover Actins can be classified in three pairs: two isoforms expressed in striated muscle (skeletal and cardiac tissue), two isoforms from smooth muscle (alpha-smooth muscle predominately in vascular tissue and γ-smooth muscle in the gastrointestinal and genital tracts) and two cytoplasmic isoforms (Bertola, Ott, Griepsma, Vonk and Bagowki, 2008; Murrell, Oakes, Lenz & Gardel, 2015).

Cytoskeleton

It is believe that "all living beings are in fact descendants of a unique ancestor commonly referred to as LUCA (the Last Universal Common Ancestor)" (Forterre, Gribaldo, Brochier, 2005), even if it's just a hypothetical life form that presumably was the progenitor of the three domains of life (Archaea, Bacteria and Eukarya), LUCA probably can explain why motility become so important to species.

In this regard, the eukaryotic cytoskeleton appears to have evolved from ancestral precursors related to prokaryotic FtsZ (which is a protein encoded by the ftsz gene) and MreB (which is a protein found in bacteria that has been identified as a homologue of actin) that show 40−50% sequence identity across different bacterial and archaeal species (Wickstead and Gull, 2011).

It seems that FtsZ is plastid-derived and serves a similar role in the division of the chloroplast and/or mitochondrion that it once did in their free-living ancestors. FtsZ mediates prokaryotic cell division, and mitochondrial and plastid division in eukaryotes, by forming a dynamic ring between prospective daughter cells (or daughter organelles) (Koumandou, Wickstead, Ginger, van der Glezen, Dacks and Field, 2013).

Before cytokinesis, which is the physical process of cell division, which divides the cytoplasm of a parental cell into two daughter cells, allowing two types of nuclear division called mitosis and meiosis. Mitosis and each of

the two meiotic divisions result in two separate nuclei contained within a single cell (Cooper, 2000).

When the cytoplasmatic division of a cell produced mitosis and meiosis, originated the common ancestor and FtsZ was passed to bacteria and euryarchaea, where it is used in almost all modern species and shows surprising plasticity in composition, with the core lament-forming proteins conserved in all lineages (Forterre, 2005).

FtsZ was also used for division in the earliest eukaryotic and later evolved an actin-based machine for cytokinesis, and eukaryotic FtsZ underwent a drastic change as it evolved into tubulin. Cytoskeletal proteins probably evolved even earlier, in the common ancestor of bacteria, archaea and eukarya. FtsZ in particular is an ancient protein. FtsZ and MreB originally functioned for cytokinesis and cell shape, respectively, and they have maintained these functions across bacteria and archaea (Koumandou, Wickstead, Ginger, van der Glezen, Dacks and Field, 2013; Wickstead and Gull, 2011; Cox, Foster, Hirt, Harris and Embley, 2008). Even ciliates contain actin, ciliates are microbial eukaryotes with two types of nuclei: a germline micronucleus (MIC) and a somatic macronucleus (MAC) (Faguy, Doolittle, 1998).

Another important process that has had a very long evolution is the control of actomyosin contraction by an increase in intracellular calcium concentration which a highly conserved mechanism for generating mechanical stress in animal cells and underlies muscle contraction, cell migration, cell division and tissue morphogenesis (Poole, Lundin and Rytkönen, 2015).

This crucial process in animal muscle physiology appears to be an ancestral feature of eukaryotic cells (Tekle and Williams, 2016). However, it was necessary ATP to promote the rotor stator-type ATPase, a protein that is as universal among cells as the code, and that is unquestionably an invention of the world of genes and proteins. After that, probably as Forterre (2005) explains: "RNA played both the role of catalyst and genetic material and this could happened through several steps. After that, a new kind of cell began to have different needs while interacted with environment and eventually; actin was

needed to allow new sets of skills". As a result proteins as Actin family and genes can be found through all phylogenetic trees

Actin, myosin and calmodulin are virtually universally present in eukaryotic genomes. Myosins are composed of a heavy chain containing the motor domain converting ATP-hydrolysis into mechanical force along actin filament (with ATPase and actin-binding activities) (Newman, 2016), and usually a light-chain binding neck domain. In most myosin families, the light chains are calmodulin proteins; in others, specialized calmodulin-related proteins have evolved, such as the essential and regulatory light chains of myosin II (Luciano, Agrebi, Le Gall, Wartel, Fiegna, Ducret, Brochier-Armanet, Mignot 2011).

Phylogenetic analyses show that actin genes in the seven species could be divided into two major types of clades: orthologous group versus complex group. Codon usages and gene expression patterns of actin gene copies were highly consistent among the groups because of basic functions needed by the organisms, but much diverged within species due to functional diversification. In this sense, most vertebrates contain two genes for class IX myosins while in invertebrates a single gene for class IX myosins has been identified. The two class IX myosins in mammals, myosin IXa (Myo9a, myr7) and myosin IXb (Myo9b, myr 5), exist in multiple splice variants among species (Newman, 2016).

Much of this complexity evolved before the last common ancestor of eukaryotes. The distribution of cytoskeletal laments puts constraints on the likely prokaryotic line that made this leap of eukaryogenesis process, which is estimated to have occurred over one billion years ago (Wickstead and Gull, 2011).

With this in mind, cell origins can be grouped into two major categories; first a fusion model where an endosymbiosis event delivering the mitochondrion came extremely early, or a fusion later model where endosymbiosis occurred after development of several intracellular structures. While the second model places emphasis on a requirement for phagocytosis-like mechanisms to be present to facilitate endosymbiont

acquisition which is considerate the origin of the eukaryotic cell, and represents one of the fundamental evolutionary transitions in the history of life on earth (Gray, 2012).

In other species, such as vertebrates, cytoplasmic actins resemble actins present in numerous amoebas, yeast and slime molds. Invertebrate muscle actins are more closely related to vertebrate cytoplasmic actins than to vertebrate muscle actin isoforms. Actin isoforms specific for striated muscle tissue first evolved in primitive chordates (Newman, 2016). At the level of early amphibians or stem reptiles this gene probably duplicated, which resulted in an alpha-skeletal and a modern alpha-cardiac isoactin. The smooth muscle isoactins are believed to have evolved during later development of warm-blooded vertebrates and likely originated from an early skeletal muscle actin. Altogether, over 30 different actins have been characterized from various muscle sources, some of them having a very specialized role (Faguy, Doolittle, 1998).

When Eukaryotic cells began to convert external stimuli into membrane depolarization, which in turn triggers effector responses such as secretion and contraction, it involved a number of important and diverse cellular processes such as organelle movement, exo and endocytosis, nuclear trafficking, and chromatin remodeling, so a variety of classes of actin binding proteins are found in plants and animals that facilitate the dynamic nature that makes it one of the most dynamic features in a eukaryotic cell (Murrell, Oakes, Lenz & Gardel, 2015).

So far we can say that actin proteins family has a very important function to movement process, intra, extra and among cells. Being a very well conserved heritage from prokaryotes cells, there is no doubt that is a relevant part of the evolution of species. But, how did this happen?

Evolution of cells and movement processes

It appears that life first emerged at least 3.8 billion years ago, approximately 750 million years after Earth was formed. The first cell is presumed to have arisen by the enclosure of self-replicating RNA in a membrane composed of phospholipids. These are the basic components of all the biological membranes, including plasma membranes in both prokaryotic and eukaryotic cells (Cooper, 2000), but are also a vital, and perhaps driving, force for the transition between prokaryotic, bacterial, archaeal, and eukaryotic cellular organization was the development of a cytoskeleton (Brunet and Arendt, 2016).

However, because cells needed energy to move, the mitochondrion was likely the best machinery option. It is best known for its role in ATP synthesis by oxidative phosphorylation. In this pathway, pyruvate from glycolysis is imported into mitochondria where it is oxidatively decarboxylated to acetyl-CoA by pyruvate dehydrogenase (PDH) and fed into the Krebs cycle to produce Nicotinamide adenine dinucleotide NADH, and Flavin adenine dinucleotide FADH2, which role is to donate electrons to the electron transport chain. They both donate electrons by providing a hydrogen molecule to the oxygen molecule to create water during the electron transport chain; these reduced cofactors combine chemically with oxygen, by the electron transport chain (ETC), to produce a proton gradient across the inner mitochondrial membrane and finally reduce O_2 to H_2O (Stairs, Leger and Roger, 2015).

The proton motive force drives ATP synthesis by an F1Fo-ATP synthase. However, mitochondria are known to carry out many other metabolic and biosynthetic functions. In addition to possessing genomes that are replicated, transcribed and translated, they function in iron–sulfur (Fe–S) cluster generation (via the iron–sulfur cluster (ISC) system) of biosynthesis, amino and fatty acid, phospholipid, vitamin and steroid metabolism (Newman, 2016).

In 1998, Martin & Müller, proposed the "hydrogen hypothesis" in which they argued that eukaryotes could have risen through the symbiotic association of an anaerobic, strictly hydrogen-dependent, strictly autotrophic archaebacterium (the host) with a eubacterium (the symbiont) that was able to respire, but generated molecular hydrogen as a waste product of anaerobic heterotrophic metabolism.

The host's dependence upon molecular hydrogen, produced by the symbiont, is put forward as the selective principle that forged the common ancestor of eukaryotic cells. With this process, the ancestor of mitochondria was an H2-producing, facultatively anaerobic a-proteobacterium that formed a syntrophic relationship with a hydrogen-dependent methanogenic archaeon. In an anaerobic environment, the a-proteobacterium produced ATP by the anaerobic extended glycolysis pathway discussed above, producing Hydrogen, carbon dioxide and acetate as waste products that were consumed by the methanogen" (Martin, Müller, 1988).

Over time, the host archaeon maximized surface area contact with the symbiont (without phagocytosis) to acquire these waste products. At that point, the host–symbiont system could exist in anaerobic and aerobic environments (Stairs, Leger and Roger, 2015). This proto-eukaryote had an archaeal cytoplasm and a hydrogen- produced an organelle also capable of oxygen-dependent respiration. Later, after the major lineages of extant eukaryotes diverged from the last eukaryotic common ancestor (LECA), and aerobic and anaerobic metabolisms were differentially lost in anaerobic and aerobic lineages, respectively, generating the diversity of energy metabolism and the present-day mitochondrion-related-organelles (Martin, Müller, 1988).

The selective advantage of these changes was the ability to continue to produce acetyl-coenzyme A and eventually ATP from pyruvate (and/or malate) under hypoxic conditions commonly encountered by free-living and anaerobic eukaryotic organisms. However, the model rests on the general assumption that, in adapting to new environments, eukaryotes can acquire and express genes from prokaryotic or eukaryotic donors that allow them to better thrive (Poole, Lundin and Rytkönen, 2015), since its molecular and morphological attributes are highly conserved and have played a pivotal role in our understanding of the origin and evolution of diverse eukaryotes (Tekle and Williams, 2016).

Besides the mitochondria, centrosomes are another old innovation. They are membrane-free organelles that serve as main microtubule organizing centers in distinct eukaryotic lineages (Azimzadeh, 2014). In preparation for cell division, the centrosome duplicates, and in mitosis, the sister centrosomes act in a dominant manner to determine the essential bipolarity of the spindle. Because the purpose of mitosis is to divide a mother cell into two genetically identical daughter cells, the cell must ensure that the centrosome inherited from the previous mitosis doubles once and only once (Sluder, 2014).

Such strategies are just an example of the multiple survival tools that evolution created with a range of exquisite movement options. This is particularly interesting if it's seen in perspective. The animals (Metazoa) are one of several dozen independently arising groups of multicellular organisms. They emerged more than 600 million years ago, among cells belonging to a broader phylogenetic group, Holozoa, which also includes some present-day unicellular and transiently colonial forms (Tekle and Williams, 2016).

While plants, bacteria and virus are humble examples of motility, the transition from few cells organisms to vertebrates in water is a fundamental step in the evolution of terrestrial life and the exponential development of bones and muscles became a necessary feature. Once out of water, animals require a structural framework that can resist the newly significant effects of gravity, as well as allow effective transmission of force to the substrate to enable propulsion. In most terrestrial vertebrates, the bones of the appendicular skeleton provide this framework (Blob, Espinoza, Butcher, Lee, D'Amico, Baig, Sheffeild, 2014).

A variety of actinopterygian fish species evolved to have the ability to traverse over land using combinations of fins that are supported primarily by flexible bony rays. Some critical innovations to this transition was the evolution of a weight bearing pelvis, hind limbs and their associated musculature and movements that permit running or walking back and forth predominates in terrestrial locomotion. The fossil record reveals how the skeletal framework of the load-bearing limbs of tetrapods (animals descended from fish) has evolved, but as soft

tissues are rarely preserved within the fossil record, it can shed little light on how the accompanying dramatic alterations of the limb musculature arose developmentally (Blob, Espinoza, Butcher, Lee, D'Amico, Baig, Sheffeild, 2014).

Locomotor strategies in terrestrial tetrapods have evolved from the use of sinusoidal contractions of axial musculature, evident in ancestral fish species, to the reliance on powerful and complex limb muscles to provide propulsive force this means the adoption of the fully derived mode of hind limb muscle formation from this bimodal character state is an evolutionary innovation that was critical to the success of the tetrapod transition (Cole, Hall, Don, Berger, Boisvert, Neyt, Ericsson, Joss, Gurevich, Currie, 2011).

Nevertheless, even if muscles, nerves and somatosensory processes are a big leap in evolution terms, a central nervous system was necessary to create adaptive strategies. The origin of the nervous system was an evolutionary event that fundamentally changed how control is achieved within a multicellular body.

Nervous System: controlling the movement process

The human brain weights an average 1.2–1.8 kg and has about 100 billion neurons (Jékely, Kejzer and Godfrey-Smith, 2015). While, the origins of brain and central nervous system (CNS) is thought to have occurred before the Paleozoic era, 540 million of years ago (Strausfeld and Hirth, 2016), the origin and diversification of the animals occurred during the so-called Cambrian explosion, and this period is tied into the evolution of their important organ systems. In this sense, the nervous system must be considered to be of extreme importance, not only because among animals apart from sponges, arthropods, chordates and placozoans shared similarities in brain and nervous system organization, but also because of the role it plays in coordination, sensing and many other aspects of the life of an animal (Budd, 2015; Kass, 2013).

As result of such an event, early mammals evolved from mammal-like synapsids over 200 million of years,

but they differed from mammals, as Kass (2008) explains they had "low-resolution olfaction, poor vision, insensitive hearing, coarse tactile sensitivity, and unrefined motor coordination, together with limited sensorimotor integration" (Hejnol and Lowe, 2015).

Early mammals had small brains in proportion to their body size, much larger forebrains, greatly expanded olfactory (piriform) cortex, a dorsal cap of neocortex, an expanded cerebellum, and a thicker spinal cord, and these brains contained rather simple sensorimotor systems. They also had auditory specializations that would allow high frequency hearing, and possibly they alone could use high frequency communication calls. Later, mammals emerged from mammal-like reptiles about 200 million years ago and radiated into the over 3,500 surviving (living) (Collin, Davies, Hart and Hunt, 2009).

Some believe that the similarities between distantly related animals during the development of their central nervous system could be the expansion of a central nervous system with a single centralized medullary cord and a partitioned brain is homologous across bilaterians, since a morphologically and molecularly tri-partitioned brain connected to a ventral nervous system present in the last common ancestor of protostomes and deuterostomes, such idea also implies a secondary reduction in animal lineages that have a much simpler organization of their nervous system (Bielecki, Høeg, Garm, 2013).

From a phylogenetic perspective, the first general consideration of the origin of the nervous system is whether or not it had one or more separate origins. It has been traditional to regard nervous systems as having evolved once only, at the base of the so-called Epitheliozoa essentially all of the animals apart from the sponges. The best evidence we have for early nervous system remains the Ediacaran to Cambrian trace fossil record, but its increasing elaboration across the boundary cannot be simply read as increasing nervous system complexity, as ecological opportunity also seems to play a role in determining trace fossil morphology (Kass, 2013).

Under this context, we believe that motility has diverse impact in human development, and species evolution,

not only from a genetic, and cultural perspective but also as evolving trigger to advance as specie. Movement is related with processes as learning, memory and sleep, because many neurological networks are shared for all this systems (Dzib-Goodin, Sanders, Yelizarov, 2017; Dzib-Goodin, and Yelizarov, 2016; Lotem and Halpern, 2012). This links are vital to cognitive skills and learning in order to help species to adapt to the environment.

Additionally, to the central nervous system, considerations about the origin of sensory organs are crucial to an understanding of brain evolution and movement process. Among sensory systems, the origin of eyes has dominated discussions and theories about what selection pressures have driven eye evolution; from the first appearance of photosensitive receptors to the appearance of single lens eyes and compound eyes and their underlying circuits. For example, color vision is inferred to have evolved in the earliest vertebrates more than 540 million of years, providing the basis for color discrimination in all extant vertebrate classes found today (Bielecki, Høeg, Garm, 2013).

The evolutionary constraints placed upon the shape, light responses, spectral sensitivity and molecular structure of photoreceptors in early vertebrates and their role in visual behavior. Paleontological evidence from the Silurian and Devonian periods shows that the lateral eyes of the ancestral vertebrates were capable of image formation and were rotated within their orbits by seven extraocular eye muscles (Perrin, Sonnemann, Ervasti, 2010).

This is expected because all sensory systems desensitize due to receptor adaptation, and visual systems are no different. Also, since photo adaptation occurs at the cellular level of photoreceptors it is an unavoidable feature in metazoan vision. Thus, all examined photoreceptors adapt to constant visual stimuli and counterstrategies are necessary to prevent image fading or blindness. The best-known mechanism to avoid adaptation is the fixational eye movements in mammals (tremor, drift and microsaccades), which continuously refocus and refresh the retinal image. The movements are generated by an oculomotor system and since they have a blurring effect on the retinal image, additional neural specializations in post-processing pathways have evolved to eliminate the periods of movement These mechanisms are very powerful, but also very costly in both energy and neural capacity, and thus, not available for animals with less elaborate processing capabilities (Collin, Davies, Hart and Hunt, 2009).

Of course it is not possible to forget the fine auditory system, which seems to be particularly sensitive to perturbations of cytoplasmic actins, perhaps because actin is a key structural component of auditory hair cells, which convert sound waves to neural signals. Hair cells are housed in the organ of Corti, both of which feature an intricate architecture that is required for proper function. The organ of Corti consists of three rows of outer hair cells (OHCs) and one row of inner hair cells (IHCs) together with several types of support cells. This ribbon-like structure runs longitudinally along the length of the cochlea. Outer hair cells function to improve sensitivity to sound while IHCs are the auditory receptors Both cell types are topped with specialized structures called stereocilia, which are elaborated microvilli formed from a mixture of b-actin and c-actin filaments that are organized in a tightly bundled para-crystalline array (Chakraborty and Jarvis, 2015).

As a result of the sensory motor systems, the nervous system diversified. The human–chimpanzee bifurcation is most commonly estimated at 5–6 million of years although some researchers believe this divergence could be greater than 7–9 million of years (Kass, 2013).

The primates brain evolution

The large size and complex organization of the human brain makes it unique among primate brains. In particular, the neocortex constitutes about 80% of the brain, and this cortex is subdivided into a large number of functionally specialized regions, the cortical areas. Such a brain mediates accomplishments and abilities unmatched by any other species (Dzib-Goodin and Yelizarov, 2016).

Historically, the origin of nervous systems has been discussed in the light of two different conceptual models. We call these the input–output (IO) and internal coordination (IC) models. The two models emphasize two different aspects of the nervous system as a control device. According to IO models, the main role of the nervous system is to receive sensory information and process it to produce meaningful motor output (Hashimoto, Ueno, Ogawa, Asamizuya, Susuki, Cheng, Tanaka, Taoka, Iwamura, Suwa and Iriki, 2013).

A distinction between IC and IO roles can be made, and often IC and IO functions are superimposed onto each other. As for behavior, also for physiological functions we can distinguish three types of effectors that the nervous system can influence, cilia, muscles and glands. On the other hand, some physiological processes require internal coordination which nervous systems make possible. Complex, muscle-driven physiological processes, such as peristaltic contractions to move the content of the gut or heartbeat, require IC systems to control them, like those that need perception of light, especially by melatonin-based signaling systems. Melatonin signaling is very old system, seen in cnidarians and annelids as well as chordates, and it can control both behavioral changes and several aspects of physiology, including sleep, appetite and reproduction (Jékely, Kejzer and Godfrey-Smith, 2015).

While an IO model tends to assume an operational effector system and addresses how this system is to be put to use, an IC model highlights the evolutionary shift involved in generating new multicellular effectors. In particular, the use of extensive contractile tissues (muscle) by large organisms is an important evolutionary invention. Achieving organized movement in a muscle is a demanding task that should not be taken for granted, as sometimes happens in discussions employing an IO framework.

This makes sense because ciliary beating is used for locomotion in a wide range of small organisms, and also has other uses. Inside a sponge, for example, cilia are used to create water flow to enable access to food

and oxygen, so the cilia must have their movements coordinated, and this is a first context in which an IC function might be relevant. Once coordinated ciliary motion exists in an organism, control devices may modify the activity of the cilia. Thus cilia can become part of an IO system. Phototactic steering is an important IO function that is specific to locomotion and can be found even in many metazoan larvae (Jékely, Kejzer and Godfrey-Smith, 2015).

However, the brain of the genus homo emerged in the early Pleistocene, just after 2 million of years, and the first representatives of the Homo Sapiens appear in the fossil record around 200 thousand years ago. The scarcity of relevant fossils in the intervening period makes interpretation difficult, but some evolutionary patterns over time are evident for example, the pelvises of early Homo, although similar in overall form to earlier hominids, have derived traits that distinguish them from australopithecines. Many of these are probably related to changes in locomotor behavior (García-Grajales, Jérusalem, Goriely, 2017).

In order to process so many new features, the nervous system needed an adaptive force. Neuronal growth is the key process necessary to establish the neuronal network during neurogenesis. Besides its vital role, neuronal growth also fulfills crucial functions in human brain plasticity and neuronal regeneration are an important characteristic (Kass, 2012a).

In the early stages of neuronal development, multiple neurites sprout from the soma up to several micrometers, led by highly dynamical hand-shape terminations called growth cones (GCs). Eventually, one neurite specializes into the axon, while all the other neurites become dendrites, and this was possible thanks to Paralemmin-1 which is a protein that stimulates cell expansion implicated in plasma membrane dynamics, the development of filopodia, neurites and dendritic and the extension of filopodia and processes in fibroblasts, spines. A family of proteins can be found on vertebrates, the identification and annotation of paralemmin genes in the different vertebrate genomes revealed that they have a common gene organization

(Khaitovich, Weiss, Lachmann, Hellmann, Enard, Muetzel, Wirkner, Ansorge, Pääbo, 2004).

As a result of the changes in motility, in neurons, extremely long neurites filled with G-actin must regulate the formation of F-actin in response to dynamic events such as synapse formation or axon guidance during sensation of chemo-attractive/chemo-repulsive cues. In addition, formation of ectopic F-actin must be suppressed to avoid physical blockages that could impede important transport functions within relatively thin neurites and produce deleterious cellular effects (Kass, 2004).

For example, neurites contain a microtubule-rich cytoskeleton that provides a physical scaffold for delivery-both in anterograde and retrograde directions-for cargoes required to maintain proper neuronal function. Energy-dependent molecular motors, including dyneins and kinesins are ATPases that physically help deliver targeted cargoes by directional movement along these microtubules. In particular, the kinesin superfamily protein KIF5 can transport diverse cargoes including membranous organelles, cytoskeletal proteins, and mRNAs (Khaitovich, Weiss, Lachmann, Hellmann, Enard, Muetzel, Wirkner, Ansorge, Pääbo, 2004).

Once an axon is fully established, it can advance long distances navigating through a pool of chemo-mechanical cues and obstacles to find its final location (Kass, 2004), but physical forces are one of the main actors throughout all scales in brain development, from molecular assembly of the neuron organelles to the final construction of the whole organ. The main structural scaffold of the neuron, the cytoskeleton is an evolving dynamic polymeric structure that is actively involved in axonal outgrowth (Kass, 2004).

The cytoskeleton is composed of three main types of filamentous polymers: F-actin, microtubules and neuro- filaments. Neurofilaments are passive and apolar polymers. Despite being the most abundant cytoskeletal filaments in the axon, they are not believed to contribute to axonal growth. The two other polymers, F-actin and microtubules, are highly dynamic and polarized. The former polymerizes at one end (barbed-end) by

addition of G-actin and depolymerizes at the other end (pointed-end) by removal of monomers, while the latter polymerizes at one end (plus-end) by addition of tubulin dimers and depolymerizes at the other end (minus-end) by removal of monomers. While microtubules are the stiffest cytoskeleton components and F-actin are less rigid on their own, the latter are able to build organized stiff structures thanks to the presence of high concentrations of crosslinkers. Their complex interactions as well as their relations with the surrounding structures and associated motor proteins (e.g., Dynein or Kinesin for microtubules or Myosin II for F-actin) are crucial for proper axonal development, they also are heterogeneously distributed along the axon domain (Kass, 2012a).

This is because active matter systems, in particular the cell cytoskeleton, have the distinct ability to convert energy from their surroundings into mechanical work, which gives rise to them having highly dynamic properties and can dynamically respond to chemical and mechanical cues to control cell structure and shape, playing a central role in many higher-order cellular processes

The dynamic nature of the cytoskeleton allows the cell to respond to both chemical and mechanical cues, providing complex feedback mechanisms for growth and remodeling. Using molecular motors, the cytoskeleton can harness energy from ATP hydrolysis, converting it into mechanical work that can drive the system into configurations not possible with thermal motion alone. Along with the inherent nature of cytoskeletal filaments, which can assemble or disassemble rapidly due to chemical species gradients or regulatory signaling cascades, this energy consumption allows the cytoskeleton to dynamically respond to a range of extracellular stimuli on varying timescales (Dzib-Goodin and Yelizarov, 2016).

Of course, different anatomical brain structures appeared at different times during vertebrate evolution. As a result, the vertebrate brain is proposed to consist of three basic divisions, with the spinal cord and brainstem (hindbrain, midbrain and thalamus) having more conserved organization, and the telencephalon more divergent organization, it consists of three major

subdivisions, with the pallidum and striatum having more conserved organization and the pallium or cortex a more divergent organization. The pallium is largely layered in mammals, and mostly nuclear in birds, reptiles and other vertebrates, but with divergences among them. Some changes may have occurred with the emergence of the telencephalon during the invertebrate to vertebrate transition, indicating that the central nervous system has been an important target of selection (Khaitovich, Weiss, Lachmann, Hellmann, Enard, Muetzel, Wirkner, Ansorge, Pääbo, 2004).

At the molecular level, the view that most changes are due to Darwinian selection was challenged by Kimura's neutral theory of molecular evolution (cited by Khaitovich, et. al, 2004). This theory states that the vast majority of differences seen in nucleotide and amino acid sequences within and between species have no or only minor selective effects. Consequently, their occurrence within a species and the fixation of differences between species are primarily the result of stochastic processes. In fact, even at the level of morphology, it has been argued that many features are not adaptive, but instead result from physical constraints or historical accidents (Kass, 2004).

As brains get bigger or smaller in evolution, different design problems arise. The main reason for this is that the fundamental unit of brains, the neuron, does not scale very well. Rather than small brains having small neurons, they have fewer, and large brains have more further increases in brain size produce less and less gain in computational power. A partial solution is for large brains to become more modular by increasing the number of areas and subdivisions of areas in order to reduce the number of long connections (Galván-Celis, Pechonkina, Slovec, Dzib-Goodin, 2015; Hofman, 2014).

Thus, as hominid brains got larger, they should also have become more modular. The best example of this in the human brain is the evidence that some functions are uniquely lateralized so that they are largely mediated in one cerebral hemisphere, and probably language can be the best example (Galván-Celis, Pechonkina, Slovec,

Dzib-Goodin, 2015; Khaitovich, Weiss, Lachmann, Hellmann, Enard, Muetzel, Wirkner, Ansorge, Pääbo, 2004). Of course, lateralization reduces the need for large numbers of long, thick axons coursing between the two cerebral hemispheres motor cortex in humans appears to be more focused on fine digit movements, and of course there is the specialization of ventral premotor cortex of the left cerebral hemisphere for speech (Mendoza, Merchant, 2014).

Part of the reason to these changes is because, early anthropoids diverged from other primates during 65–90 million years to exploit the diurnal niche eating fruit, buds, and the occasional insect in the terminal branches of tropical forests, they had an expanded posterior parietal sensorimotor cortex that included several fields involved in visual, auditory, and somatosensory guidance of motor plans, and the frontal motor regions, as parts of a sensorimotor network, were enlarged and subdivided in early primate (Galván-Celis, Pechonkina, Slovec, Dzib-Goodin, 2015; Kass, 2008; Khaitovich, Weiss, Lachmann, Hellmann, Enard, Muetzel, Wirkner, Ansorge, Pääbo, 2004).

Eventually primates emerged over 80 million years ago as a branch of the Euarchontoglire superclade, they were small, arboreal, and nocturnal. They fed on small insect and vertebrate prey, buds, and fruit Primates constitute an order of mammals that is extremely varied in brain size. This branch included several lines of archaic primates that became extinct, and the stem euprimates that led to the present-day galagos, lorises, tarsiers, and the greatly varied anthropoid monkeys, apes, and hominids (humans and extinct species more closely related to us than chimpanzees) (Kass, 2004).

Their brains were moderately expanded, and not much different in size and proportion to body size than the brains of extant prosimian primates (lemurs, lorises, and galagos). Their eyes were large, and frontally directed, and their temporal cortex was enlarged. Thus, vision was obviously important, and adaptations for life in the fine branches of trees suggested that their neural systems for

eye-hand coordination were well developed to subserve reaching for food items while clinging to unstable branches (Kass, 2012a).

The closest living relatives of primates are the Scandentia (tree shrews) and Dermoptera (flying lemurs) of the Archontan branch of Euarchontoglires. The more distant Glires branch includes rodents and lagomorphs. While modern humans and chimpanzees are separated from a common ancestor by only a few million years, our brains are three times larger, with most of this increase over the past 2 million years of hominin evolution. Only relatively recently, within thousands of years, we have become the only surviving species within the formerly varied hominin branch. The earliest disputed hominin is Sahelanthropus tchadensis, dated to approximately 7 million of years. The emergence of the H. erectus sensulato in East Africa represents a fundamental turning point in hominin evolution (Maslin, Schultz and Trauth, 2015).

The relative expansion of the cerebellum in primates together with stereopsis and elaboration of the visual system presumably underpins primates' fine viso-motor control and manual dexterity. For example, smooth-pursuit eye-movements in primates are based on a unique cortico-cerebellar pathway that evolved together with foveal vision. All major cortical regions, for example beyond motor cortex and including frontal and prefrontal areas, have reciprocal connections with the cerebellum (Kass, 2013).

These cortico-cerebellar loops form multiple, independent anatomical modules which are architecturally quite uniform (Kass, 2012b).

A good example of this process can be experimented when something is touched with a finger, since this simple act can stabilize a person who is about to lose his/her balance. The spatial acuity of the fingertip is better defined than that of the vestibular system and it is sensitive enough to detect small body sway. Tactile feedback from the finger is essential for reducing sway responses, yet no effects of fingertip-contact forces on postural sway previously have been reported. The fact that postural sway induced by vestibular stimulation is reduced by finger touch suggests that somatosensory inputs can modulate the vestibular processes that control postural balance. Bimodal neurons in the vestibular cortex converging vestibular and somatosensory inputs may explain those somatosensory modulatory effects on vestibular responses. The vestibular cortex may combine multimodal reference frames to maintain the unity of the spatial experience (Barton, 2012).

When Homo sapiens appeared, many more motor behaviors had to be controlled by the nervous system. Culture began to have an impact on the strategies to adapt to the environment, so it opens the door to cognition processes (Stout and Chaminade, 2012). Using tools probably lead to more fine abilities necessaries to survive, but certainly is not the only one reason, because some other mammals use tools to get food, and by some reason didn't forced to those species to the level of human beings.

Human brains: cognition and its relationship with motor control

Speech and tool use are both goal-directed motor acts (Stout and Chaminade, 2012). The classical definition of the tool is restricted to external objects held by the hand and interacting with the external environments, but modern humans also use tools to extend or externalize our existing sensory organs, or to support the detection of information that is outside our natural sensory range This leads to the perception of our own natural intransitive movement as transitive, this is the acquisition of a sense of the self (as the subject), and leading to the movement of ourselves or our body parts perceived as objects (Iriki and Taoka, 2012).

Producing words and vocal learning, are a critical component of spoken language acquisition, and they are defined as the ability to modify acoustic and/or syntactic features of sounds produced, including vocal imitation and improvisation, like other motor actions, implies execution and comprehension from neural circuits integrating sensory perception and motor control, but they were

linked as a need to survive and communicate strategies (Galván-Celis, Pechonkina, Slovec, Dzib-Goodin, 2015; Stout and Chaminade, 2012; Iriki and Taoka, 2012).

An obvious difference between speech and tool use is that the former typically occurs in an auditory and vocal modality, whereas the latter is predominantly visuospatial, somatosensory and manual. Nevertheless, there are important similarities in the way speech and tool-use networks are organized, including strong evidence of functional–anatomical overlap in inferior frontal gyrus and, less decisively, in inferior parietal and posterior temporal cortex. The similarity of cognitive processes and cortical networks involved in speech and tool use suggests that these behaviors are best seen as special cases in the more general domain of complex, goal-oriented action (Stout and Chaminade, 2012).

The evolutionary intensification of tool-use may include the integration of visual, and symbolic-abstract information processing leading to an emergence of a novel functional brain area for conceptual understandings of tool functions, fulfilling the sufficient condition for the boost of complex human tool-usage (Hashimoto, Taoka, Obayashi, Hara, Tanaka, Iriki, 2013). This can be the reason why areas of the neocortex that are particularly large in the human cortex, for example the prefrontal granular cortex (PFC) or language related Broca and Wernicke areas, which are considered as analyzers for integration of information from various sensory and motor areas (Galván-Celis, Pechonkina and Dzib-Goodin, 2014).

In this regard, Corballis (cited by Jablonka, Ginsburg and Dor, 2012) explains that motor control involved in learning and teaching tool manufacture is the platform for the evolution of increasingly complex communication, too, emphasizes the role of motor control, arguing that the evolution of language may have had its origins in the control of manual and oro-facial gestures (and only later of vocalizations). He proposed that the voluntary motor control that was necessary for tool making made gestural communication easy, and this was generalized to oral movements, which then led to speech.

Other, non-mutually exclusive ideas are that motor imitation, necessary for the manufacturing of complex Acheulean tools, was a prerequisite for the evolution of syntactic language: the hierarchical recursive organization that enables the stepwise combination of motor units necessary to manufacture complex tools is the suggested basis of hierarchical and recursive syntax, in which communication signs are embedded and combined into larger semantic representations (Iriki and Taoka, 2012).

In broadest terms, language can be divided into a conceptual–intentional system that deals with thoughts and meaning, and a sensorimotor system that deals with the acoustic analysis of speech sounds and their production (Galván-Celis, Pechonkina and Dzib-Goodin, 2014; Rakic, 2009).

This implies that once a novel cognitive demand, such as incorporation of motor tools into the body schema, has become embedded in the environment, modifications of brain structure would be induced automatically through the normal developmental processes in succeeding generations. The occurrence of such a plastic response during the lifespan as a result of behavioral modifications, lie within the existing adaptive capacity of individuals, and its subsequent consolidation (under selection acting on changing gene frequencies), as a default state that is stable over generations (Iriki and Taoka, 2012).

Eventually, other processes could come to use the motor areas that have changed as an effect of culture perspective, and example of this can be writing and reading processes, since they are new learnings in the history of humankind (Galván-Celis, Pechonkina and Dzib-Goodin, 2014).

Vocal control

Interestingly, vocal learning is a rare trait, so far discovered in five distantly related groups of mammals (humans, bats, elephants, cetaceans (dolphins and whales) and pinnipeds (seals and sea lions) and three distantly related groups of birds (parrots, songbirds and hummingbirds). The independently evolved lineages of

vocal learning birds and humans, share distinct forebrain pathways that control the acquisition and production of learned vocalizations. Within these pathways, all three avian lineages contain seven cerebral (telencephalic) vocal nuclei and several thalamic nuclei (Scharff and Petri, 2011).

These nuclei, best characterized in songbirds and parrots, are distributed between two sub pathways 1a): (i) the vocal production, or posterior, pathway that influences the production of learned song, which includes an arcopallium nucleus (songbird RA (robust nucleus of the arcopallium), parrot AAC (central nucleus of the anterior arcopallium), hummingbird VA (vocal nucleus of the arcopallium), analogous to the laryngeal motor cortex (LMC) in humans that makes a specialized direct projection to brainstem vocal motor neurons (MN), which in turn controls the vocal organs, the syrinx (birds) and larynx (humans); and (ii) the vocal learning, or anterior, pathway that is primarily responsible for vocal imitation and plasticity, which forms a pallial–basal ganglia–thalamic loop (Dzib-Goodin, Yelizarov, 2016), analogous to such loops in the mammalian brain that presumably include Broca's speech area in humans. The song and speech regions in both these pathways are embedded in or adjacent to non-vocal motor brain areas. These non-vocal motor regions are present in other vertebrate species examined thus far, and are thought to be involved in the production and learning of non-vocal motor behaviors (Chakraborty and Jarvis. 2015).

In this evolutionary scenario genes were important, the expression of FoxP2, which is a Fork head box protein P2 (FOXP2) is a protein that, in humans, is encoded by the FOXP2 gene, and it is required for proper development of speech and language (Dzib-Goodin, Sanders, Yelizarov, 2017). During the evolution of vocal learners, once the striatum got connected to other regions necessary for vocal learning to occur, FOXP2 mutated in humans to become human specific and this might have affected neural transmission, and in Area X of the striatum thus became useful for sensory motor integration or precise timing of vocal gestures as supposed to other motor learning tasks in adjacent non-vocal circuitry cells (Scharff and Petri, 2011). This would be a two-hit scenario of FOXP2 's role in language evolution, circuit changes predating gene function changes (Galván-Celis, Pechonkina, Slovec, Dzib-Goodin, 2015; Galván-Celis, Pechonkina and Dzib-Goodin, 2014).

The shift of body-space structure associated with the emergence of hominin bipedalism may have further pushed this trend forward to give this area, and the extended opercular cortex, further resources. Such neural enhancement (construction of the neural niche) happened to enable the processing of abstract information, detached from actual physical constraint, by applying and re-using existing principles for spatial information processing to realize novel mental functions (construction of the cognitive niche), ultimately leading to language. Purposeful manipulation of the body image in space, require for tool use, would have accelerated interactive links between the neural and cognitive niches, and tool use requires transformation of various bodily and spatial coordinates, as well as logical and sequential relations of action components (Dzib-Goodin, Yelizarov, 2016).

Tools represent materialized cognitive brain functions. They have been created one after another and incorporated into hominid habitats as constituent elements (construction of the ecological niche). A human-modified environment puts pressure on succeeding generations to adapt to it, perhaps by acquiring further resources for the relevant organs. Epigenetically induced plasticity (including developmental or learning mechanisms) would participate in such processes (Dzib-Goodin, Sanders, Yelizarov, 2017), so extra genomic information could be transmitted between generations via mutual interactions among ecological, neural and cognitive domains of niches, which may have contributed to hominid evolutionary processes. This scenario would locate the human brain as part of an evolving holistic ecosystem (Iriki and Taoka, 2012; Godfrey-Smith, 2012).

Movement process and adaptation to the environment

Once tools and language began were added to cognitive processes, after modern humans left sub-Saharan Africa around 50 000–100 000 years ago, anatomically have quickly occupied extremely diverse environments. Human populations were exposed to further environmental changes resulting from cultural innovations, such as the spread of farming, which gave rise to new selective pressures related to pathogen exposures and dietary shifts. In addition to changing the frequency of individual adaptive alleles, natural selection may also shape the overall genetic and brain architecture of adaptive traits (Olson, Knoester, Adami, 2016).

In this sense, cultural evolution is a domain in which individual cognition meets population-level dynamics. Evolution by natural selection is change in a population due to variation, heredity and differential reproductive success This is usually seen as a micro-evolutionary process acting on organisms, but the criteria required are abstract; genes, cells, social groups and species can all, in principle, enter into change of this kind. For any objects to be units of selection in this sense, they must be connected by parent offspring relations and must have the capacity to reproduce (Godfrey-Smith, 2012).

In this scenario animal-grouping behavior, had important implications for social intelligence, collective cognition, grouping behaviors are pervasive across all forms of life, Swarming is one example of grouping behavior, where animals coordinate their movement with conspecifics to maintain a cohesive group. Swarming may improve matting success, increase foraging efficiency, or enable the group to solve problems that would be impossible to solve individually, plus there is evidence of cerebellar expansion and involvement in diverse cognitive functions suggests that the well known link between neocortex size and social group size (Barton, 2012).

Furthermore, swarming behaviors are hypothesized to protect group members from predators in several ways. For example, swarming can improve group vigilance, reduce the chance of being encountered by predators, and dilute individual risk of being attacked, enabling an active defense against predators, or reduce reducing predator attack efficiency by confusing the predator (Olson, Knoester, Adami, 2016).

Equally important was to move efficiently into the physical space, and Darwin (cited in Kivell 2015), first proposed that the introduction of bipedalism was directly linked to tool use as it freed the hands from the constraints of locomotion. So, the association between motor function and cognition can be understood, in part, in the context of the evolution of human bipedalism, which served as a significant basis for the evolution of the human neocortex as it is among the most complex and sophisticated of all movements (Jeong and Di Rienzo, 2014).

This gave humans a unique ability to harness gravitational forces as a direct result of the existence of the upright position. The basis of the continuance of this genetic mutation is based on the notion that bipedalism had created larger pools of neurons. It is argued that the same evolutionary process has allowed us to develop the binding of the motor system into synchronous, rhythmic, purposeful movement, which expanded to eventually allow for cognitive binding and consciousness (Leisman, Moustafa and Shafir, 2016).

It is impossible to forget that the human pelvis is a remarkable structure that plays a central role in many critical biological processes, most notably bipedal locomotion, thermoregulation and parturition (childbirth). Each of these processes is essential enough to survival and reproductive success as to be under strong pressure from natural selection. As a result, the fossil record of the evolution of the human pelvis over the past 4.5 million years reveals a profound story concerning selective priorities during different phases of human evolution, and elucidates, the essential constraints that formed our modern anatomical condition. Pelvic anatomy impacts human performance. To walk upright in an energetically efficient manner with a minimal risk of injury, the pelvis must be robust and have a shape that maximizes muscle, control arms and minimizes load (Gruss and Schmitt, 2015).

This advance allows humans to move further, and search harborage, food and other groups. Although memory of food locations and higher cognition may limit the benefits of random walk strategies (Dzib-Goodin, Sanders, Yelizarov, 2017), so called Lévy walks may have arisen with the evolution of a hunting and gathering lifestyle in human ancestors. Lévy walks are a random walk search strategy used by a wide variety of organisms when searching for heterogeneously distributed food (Raichlen, Wood, Gordon, Mabulla, Marlowe and Pontzer, 2014). This type of search involves mostly short move steps (defined as the distance traveled before pausing or changing direction) combined with unusual longer move steps (Smouse, Focardi, Moorcroft, Kie, Forester and Morales, 2010).

This movement pattern may be fundamental to how humans experience and interact with the world across a wide range of ecological contexts, and it may be adaptive to food distribution patterns on the landscape, which previous studies suggested for organisms with more limited cognition. Lévy walks may have arisen with the evolution of a hunting and gathering lifestyle in human ancestors. The widespread use of this movement pattern among species with great cognitive variation suggests an important link between foraging patterns across different organisms, including humans (Raichlen, Wood, Gordon, Mabulla, Marlowe and Pontzer, 2014).

As a result, larger regions of posterior parietal cortex and frontal motor cortex are parts of networks devoted to producing different sequences of movements. Motor areas include primary motor cortex, ventral (PMv), and dorsal (PMd) premotor cortex, the supplementary motor area (SMA), and the frontal eye field (FEF). Somatosensory areas include the four areas of anterior parietal cortex. Primary motor cortex and dorsal and ventral premotor areas are widely recognized as valid cortical areas, and each of these areas has a somatotopic representation of small movements of body parts (Kass, 2008; Kass, 2012b). These areas are compromise in movement disorders such as apraxias (Murillo Duran, 2007).

Tools manipulation

At the same time, primate manual maneuvering, including those on experienced human stone tool, have revealed three manipulative abilities considered unique to the human hand The first is precision handling: a) the ability to rotate and manipulate objects within one hand using the thumb and fingertips. Other primates typically need to use the palm as well or their other hand, a foot or the mouth to manipulate an object into the desired position, b) The second is forceful precision gripping, in which the pads of the thumb and one or more of the fingers are able to forcefully stabilize or manipulate an object, and at the same time withstand large external forces, such as when knapping a stone tool (Kivell, 2015).

Other primates are capable of precision grips, typically tip-to-tip or pad-to-side grips between the thumb and index finger, but these are not generally done with strong force; c) The third uniquely human manipulative ability is power squeeze gripping of cylindrical objects in which the fingers grip the object diagonally across the palm and the thumb is either wrapped around the object or is in line with the forearm, such as when using a hammer ((Kivell, 2015).

Other primates are capable of power grips (using the palm) or diagonal hook grips (fingers usually stabilized against the palm), but neither provide the same control that the power squeeze grip does in humans In this sense, perhaps the most critical aspect to the unique manipulative abilities of humans is our intrinsic hand proportions (relative length of the thumb and fingers). The fifth digit is also particularly important during stone tool-related behaviors, because the fifth digit stabilizes the dominant hand during power squeeze grips and precision grips (e.g. of the core during the strike of the hammer stone), as well as during precision grips of the non-dominant hand when maneuvering an object within the hand to find the desired position (Smouse, Focardi, Moorcroft, Kie, Forester and Morales, 2010).

However, all this skills adapted over human development, lead to distinctions between cognition, as

a process of interpreting and integrating information about the outside world, the perceptual information that this process is about, and the motor commands that represent the output of cognitive processes. More recently, these distinctions have been broken down by the acknowledgement that cognition is best conceived as a set of processes mediating the adaptive control of bodies in environments (Barton, 2012).

Even if most animals are capable of acquiring, storing and using information about the landscapes they inhabit, knowledge of the environment can potentially reduce uncertainty about the location and availability of resources, and even allow for the anticipation of danger. Although little is known about how animals actually store and use spatial information, and perhaps a more realistic form or reinforced model for animal movement would allow the possibility of returning to any previously visited place even if such locales are outside the current perception area (Dzib-Goodin, Sanders, Yelizarov, 2017; Smouse, Focardi, Moorcroft, Kie, Forester and Morales, 2010).

This means that learning structure of time and space is challenging, and how it can be simplified by the joint action of learning and data-acquisition mechanisms; but they all require much memory and computation (Dzib-Goodin, Sanders, Yelizarov, 2017; Forterre, Gribaldo, Brochier, 2005).

Both cognitive and motor functions require the learning of sequential actions. These sequences are most optimized with control by specialized networks mediated by both executive function and automaticity, because learning complex sequences requires adequately functioning executive processes, this have seen because activations at varying levels of complexity have demonstrated overlap in the supplementary motor cortex and other brain regions, such as the cerebellum, basal ganglia premotor cortex, thalamus, ventrolateral premotor cortex, and precuneus, with increased activations at increased levels of complexity (Leisman, Moustafa and Shafir, 2016).

Conclusion

This paper is just a brief and not exhaustive view of movement process as a key of evolution of species and human cognition, from prokaryote to eukaryote and human cognition. Millions of years have been needed to draft biology models of our specie.

From this perspective, movement process is not only important in large scale of the universe, since it keeps galaxies and planets in a perfect dance, but it has an impact into cells, in order to create a diversification of functions, adaptation and physical features.

One scenario explored is that phagocytosis could be a key to change the evolutionary rhythm of life, and actin proteins created new options to motility, that is why a globular major component of the cellular cytoskeleton and one of the most abundant cellular proteins.

However, It was needed still a long period of time before see a primitive nervous system, probably because the advance of the sensory processes, that beside motor behavior began to create the neuronal networks in the first nervous systems that is possible to appreciate among different species. As a result the human brain with a sensory motor system capable not only to understand the environment, but also manipulate its own resources to create adaptive answers to the environment.

Once that human brain was capable to recognize itself is physical space and time, walking create a cultural revolution allowing even more connections, and allowing memory to create marks to recognize the environment. Some believe thanks to the use of tools, communication began in other ways more than just calls, and this create a cognitive niche to connect with the rest of the human.

We have explored in other articles than memory was result of movement, so of course explains why is so important to learning process. From psychological standpoint, several authors have claimed that movements seen as physical activity are important to learning process, but in our perspective, they are not capable to explain why this relationship is so important to human brains.

That is why this complex process must be seen from different perspectives, from microbiology, genetic, evolution, cultural, cognitive, clinic and even artistic point of view, and certainly each area has many more to say, because it is, from our perspective, very important to understand how cognition built human brains, that is just one example of evolution of species.

We deeply believe human brain is not the last draft of evolution, cognitive processes have been modulated based environmental needs and those changes that prove to be important over the population will become part of the repertory and structures of the brains. This is not a human design, but a species mechanism to survive.

REFERENCIAS

Ananthakrishnan, R., and Ehrlicher, A. (2007). The forces behind cell movement. International Journal of Biology Science, 3(5), 303-317.

Azimzadeh, J. (2014). Exploring the evolutionary history of centrosomes. Philosophical Transactions of the Royal Society Biological Science, 369: 20130453. http://dx.doi.org/10.1098/rstb.2013.0453

Barton, RA. (2012). Embodied cognitive evolution and cerebellum. Philosophical Transactions of the Royal Society Biological Science, 367, 2097–2107 doi:10.1098/rstb.2012.0112

Bertola, LD., Ott, EB., Griepsma, S., Vonk, FJ., and Bagowki, CP. (2008). Developmental expression of the alpha-skeletal actin gene. BioMed Central Evolutionary Biology, 8, 166 doi:10.1186/1471-2148-8-166.

Bielecki, J., Høeg, JT., Garm, A. (2013) Fixational eye movements in the earliest stage of metazoan evolution. Plos One, 8(6), e66442. doi:10.1371/journal.pone.0066442

Blob, RW., Espinoza, NR., Butcher, MT., Lee, AH., D'Amico, AR., Baig, F., Sheffeild, M. (2014). Diversity of limb-bone safety factors for locomotion in terrestrial vertebrates: evolution an mixed chains. Integrative and Comparative Biology, 54(6), 1058-1071. https://doi.org/10.1093/icb/icu032

Blombach, F., Smollet, KL., Grohmann, D., Werner, F. (2016). Molecular mechanisms of transcription initiation-structure, function, and evolution of TFE/TFIIE-like factors and open complex formation. Journal of Molecular Biology, 428(12), 2592-2606.

Brunet, T., and Arendt, D. (2016). From damage response to action potentials: early evolution of neural and contractile modules in stem eukaryotes. Philosophical Transactions of the Royal Society Biological Science, 371: 20150043. http://dx.doi.org/10.1098/rstb.2015.0043

Budd, GE. (2015). Early animal evolution and the origins of nervous system. Philosophical Transactions of the Royal Society Biological Science, 370, 20150037. http://dx.doi.org/10.1098/rstb.2015.0037

Cavalier-Smith, T. (2002). The neomuran origin of archaebacteria, the negibacterial root of the universal tree and bacterial mega classification. International Journal of Systematic and Evolutionary Microbiology, 52, 7-76.

Chakraborty, M., and Jarvis, ED. (2015) Brain evolution by brain pathway duplication. Philosophical Transactions of the Royal Society Biological Science, 370, 20150056. http://dx.doi.org/10.1098/rstb.2015.0056

Cole, NJ., Hall, TE., Don, EK., Berger, S., Boisvert, CA., Neyt, C., Ericsson, R., Joss, J., Gurevich, DB., Currie, PD. (2011). Development and evolution of the muscles of the pelvic fin. Plos Biology, 9(10), e1001168. doi:10.1371/journal.pbio.1001168

Collin, SP., Davies, WL., Hart, NS., and Hunt, DM. (2009). The evolution of early vertebrate photoreceptors. Philosophical Transactions of the Royal Society Biological Science, 364, 2925-2940. doi:10.1098/rstb.2009.0099

Cooper, GM. (2000) The cell: A molecular approach. 2nd Edition, Sunderland (MA): Sinauer Associates. Available from: http://www.ncbi.nlm.nih.gov/books/NBK9841/

Cox, CJ., Foster, PG., Hirt, RP., Harris, SR., and Embley, M. (2008). The archaebacterial origin of eukaryotes. Proceedings of the National Academy of Science of the United States of America, 105(51), 20356-20361. Doi:10.1073/pnas.0810647105.

ORIGINALES / ORIGINAL PAPERS

VOLUMEN 12. NÚMERO 1. ENE-ABR 2018. DOI: 10.7714/CNPS/12.1.204

Davidov, Y., Jurkevitch, E. (2009). Predation between prokaryotes and the origin of eukaryotes. Bioessays, 31(7), 748-757.

Dzib-Goodin, A., and Yelizarov, D. (2016). Evolución del circuito movimiento-acción y su importancia para el aprendizaje. Revista Chilena de Neuropsicología. 11(1): 35-39.

Dzib-Goodin, A., Sanders, L., Yelizarov, D. (2017). Sistemas neuro-moleculares necesarios para el proceso de memoria. Cuadernos de Neuropsicología: Panamerican Journal of Neuropsychology, 11(1), DOI: 10.7714/CNPS/11.1.204

Faguy, DM., Doolittle, WF. (1998). Cytoskeletal proteins: the evolution of cell division. Current Biology, 8(10), R338-R341.

Forterre, P. (2005). The two ages of RNA world, and the transition to the DNA world: a story of viruses and cells. Biochimie, 87(9-10), 793-803.

Forterre, P., Gribaldo, S., Brochier, C. (2005). Luca : À la recherche du plus proche ancêtre commun universel. Médecine Science, 21(10), 860-865.

Galván-Celis, V., Pechonkina, IM., and Dzib-Goodin, A. (2014). La relación entre los procesos de lecto-escritura y la música desde la perspectiva neurocognitiva. Revista Chilena de Neuropsicología, 9(1-2), 21-24.

Galván-Celis, V., Pechonkina, I., Slovec, K., Dzib-Goodin, A. (2015). Efectos cognitivos el bilingüismo coordinado en ambientes contextuales. Revista Mexicana de Neurociencia, 16(2), 39-49.

García-Grajales, JA., Jérusalem, A., Goriely, A. (2017). Continuum mechanical modeling of axonal growth. Computer Methods in Applied Mechanics and Engineering, 314: 147-163 http://dx.doi.org/10.1016/j.cma.2016.07.032

Godfrey-Smith, P. (2012). Darwinism and cultural change. The Royal Society: Biological Science, 367, 2160-2170.

Goodson, HV., and Hawse, WF. (2002). Molecular evolution of the actin family. Journal of Cell Science, 115: 2619-2622.

Gray, MW. (2012). Mitochondrial evolution. Cold Spring Harbor Perspectives in Biology, 4(9), a011403. Doi: 10.1101/cshperspect.a011403

Gruss, LT., and Schmitt, D. (2015). The evolution of the human pelvis: changing adaptations to bipedalism, obstetrics and thermoregulation. Philosophical Transactions of the Royal Society Biological Science, 370: 370:20140063. http://dx.doi.org/10.1098/rstb.2014.0063

Guljamow, A., Delissen, F., Baumann, O., Thünemann, AF., Dittmann, E. (2012). Unique properties of Eukaryote-type actin and profilin horizontally transferred to cyanobacteria. Plos One, 7(1), e29926. doi:10.1371/journal.pone.0029926.

Hashimoto, T., Taoka, M., Obayashi, S., Hara, Y., Tanaka, M., Iriki, A. (2013). Modulation of cortical vestibular processing by somatosensory input in the posterior insula. Brain Injury, 27(13–14): 1685–1691 DOI: 10.3109/02699052.2013.831128

Hashimoto, T., Ueno, K., Ogawa, A., Asamizuya, T., Susuki, C., Cheng, K., Tanaka, M., Taoka, M., Iwamura, Y., Suwa, G., and Iriki, A. (2013). Hand before foot? Cortical somatotopy suggest manual dextery is primitive and evolved independently of bipedalism. Philosophical Transactions of the Royal Society Biological Science, 368, 20120417. http://dx.doi.org/10.1098/rstb.2012.0417

Hejnol, A., and Lowe, CJ. (2015). Embracing the comparative approach: how robust phylogenies and broader developmental sampling impacts the understanding of nervous system. Philosophical Transactions of the Royal Society Biological Science, 370: 20150045. http://dx.doi.org/10.1098/rstb.2015.0045

Hightower, RC., and Meagher, RB. (1986). The molecular evolution of actin. Genetics, 114, 315-332.

Hofman, MA. (2014). Evolution of the human brain: when bigger is better. Frontiers in Neuroanatomy, 8(15), https://dx.doi.org/10.3389%2Ffnana.2014.00015

Iriki, A., and Taoka, M. (2012). Triadic (ecological, neural, cognitive) niche construction: a scenario of human brain evolution extrapolating tool use and language from the control of reaching actions. Philosophical Transactions of the Royal Society Biological Science, 367, 10-23. doi:10.1098/rstb.2011.0190

Jablonka, E., Ginsburg, A., and Dor, D. (2012). The co-evolution of language and emotions. Philosophical Transactions of the Royal Society Biological Science, 367: 2152–2159. doi:10.1098/rstb.2012.0117

Jalilian, I., Heu, C., Cheng, H., Freittag, H., Desouza, M., Stehn, JR., Bryce, NS., Whan, RM., Hardeman, EC., Faith, T., Schevzov, G., Gunning, PW. (2015). Cell elasticity is regulated by the tropomyosin isoform composition of the actin cytoskeleton. Plos One, e0126214. doi:10.1371/journal.pone.0126214.

Jékely, G., Kejzer, F., and Godfrey-Smith, P. (2015) An option space for early neural evolution. Philosophical Transactions of the Royal Society Biological Science, 370 20150181. http://dx.doi.org/10.1098/rstb.2015.0181

Jeong, C., and Di Rienzo, A. (2014). Adaptations to local environments in modern human populations. Current Opinion in Genetics & Development, 29, 1-8.

Kass, JH. (2004). Evolution of somatosensory and motor cortex in primates. The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology, 281A(1), 1148-1156.

Kass, JH. (2008). The evolution of the complex sensory and motor system of the human brain. Brain Research Bulletin, 75(2-4), 384-390. https://dx.doi.org/10.1016%2Fj.brainresbull.2007.10.009

Kass, JH. (2012a). The evolution of neocortex in primates. Progress in Brain Research, 195, 91-102 doi:10.1016/B978-0-444-53860-4.00005-2

Kass, JH. (2012b). Evolution of columns, modules, and domains in the neocortex of primates. Proceedings of the National Academy of Science of the United States of America, 109(S1), 10655–10660. www.pnas.org/cgi/doi/10.1073/pnas.1201892109

Kass, JH. (2013) The evolution of brains from early mammals to humans. Wiley Interdisciplinary Reviews: Cognitive Science, 4(1), 33–45. doi:10.1002/wcs.1206

Khaitovich, P., Weiss, G., Lachmann, M., Hellmann, I., Enard,W., Muetzel, B., Wirkner, U., Ansorge, W., Pääbo, S. (2004). A neutral model of transcriptome evolution. Plos Biology, 2(5): 0682-0689

Kivell, TL. (2015). Evidence in hand: recent discoveries and early evolution of human manual manipulation. Philosophical Transactions of the Royal Society Biological Science, 370: 20150105. http://dx.doi.org/10.1098/rstb.2015.0105

Koumandou, VL., Wickstead, B., Ginger, ML., van der Glezen, M., Dacks, JB., and Field, MC. (2013). Molecular paleontology and complexity in the last eukaryotic common ancestor. Critical Reviews in Biochemistry and Molecular Biology, 48(4), 373-396.

Leisman, G., Moustafa, AA., and Shafir, T. (2016). Thinking, walking, talking: integratory motor and cognitive brain function. Frontiers in Public Health, doi: 10.3389/fpubh.2016.00094

Lodish, H., Berk, A., Zipursky, SL., et al. (2000) Molecular Cell Biology. 4th edition. New York: W. H. Freeman;. Section 19.6, Intermediate Filaments. Available from: https://www.ncbi.nlm.nih.gov/books/NBK21560/

Lotem, A., and Halpern, JY. (2012). Coevolution of learning and data-acquisition mechanisms: a model for cognitive evolution. Philosophical Transactions of the Royal Society Biological Science, 367, 2686–2694 doi:10.1098/rstb.2012.0213

Luciano, J., Agrebi, R., Le Gall, AV., Wartel, M., Fiegna, F., Ducret, A., Brochier-Armanet, C., Mignot, T. (2011) Emergence and modular evolution of a novel motility machinery in Bacteria. Plos Genetics, 7(9), doi:10.1371/journal.pgen.1002268

Martin, W., Müller M. (1988) The hydrogen hypothesis for the first eukaryote. Nature, 392(6671), 37-41.

Martínez-Cano, DJ., Reyes-Prieto, M., Martínez-Romero, E., Partida-Martínez, LP., Latorre, A., Moya, A., and Delaye, L. (2015). Evolution of small prokaryotic genomes. Frontiers in Microbiology, doi: 10.3389/fmicb.2014.00742

Maslin, MA., Schultz, S., and Trauth, MH. (2015). A synthesis of the theories and concepts of early human evolution. Philosophical Transactions of the Royal Society Biological Science, 370, 20140064. http://dx.doi.org/10.1098/rstb.2014.0064

Medina, PMB., Worthen, RJ., Forsberg, LJ., Brenman, JE. (2008). The actin-binding protein capulet genetically interacts with the microtubule motor kinesin to maintain neuronal dendrite homeostasis. Plos One, 3(8), e3054. doi: 10.1371/journal.pone.0003054

Mendoza, G., Merchant, H. (2014). Motor system evolution and the emergence of high cognitive functions. Progress in Neurobiology, 122, 73-93.

Monshausen, GB., and Haswell, ES. (2013). A force of nature: molecular mechanisms of mechanoperception in plants. Journal of Experimental Botany, 64(15), 4663-4680.

Murillo Duran, J. (2007). Disturbios praxicos en lesiones focales de los hemisferios cerebrales. Cuadernos de Neuropsicología, 1(2) 84-114.

Murrell, M., Oakes, PW., Lenz, M., & Gardel, ML. (2015). Forcing cells into shape: the mechanics of actomyosin contractility. Nature Reviews Molecular Cell Biology, 16, 486-498.

Newman, SA. (2016). "Biogeneric" developmental processes: drivers of major transitions in animal evolution. Philosophical Transactions of the Royal Society Biological Science, 371, 20150443. http://dx.doi.org/10.1098/rstb.2015.0443

Olson, RS., Knoester, DB., Adami, C. (2016). Evolution of swarming behavior is shaped by how predators attack. Artificial Life, 22, 299–31. doi:10.1162/ARTL_a_00206

Perrin, BJ., Sonnemann, KJ., Ervasti, JM. (2010) β-actin and γ-actin are each dispensable for auditory hair cell development but required for stereocilia maintenance. Plos Genetics, 6(10): e1001158. doi:10.1371/journal.pgen.1001158

Poole, AM., Lundin, D., and Rytkönen, KT. (2015). The evolution of early cellular system viewed through the lens of the biological interactions. Frontiers in Microbiology, doi: 10.3389/fmicb.2015.01144.

Raichlen, DA., Wood, BM., Gordon, AD., Mabulla, AZP., Marlowe, FW., and Pontzer, H. (2014). Evidence of Lévy walk foraging patterns in human hunter-gatherers. Proceedings of the National Academy of Science of the United States of America, 111(2), 728–733, doi: 10.1073/pnas.1318616111

Rakic, P. (2009). Evolution of the neocortex: perspective from developmental biology. Nature Reviews Neuroscience, 10(10), 724-735. doi:10.1038/nrn2719.

Roy-Zukav, EM., Dyer, KA., Meagher, RB. (2015). Phylogenetic patterns of codon evolution in the ACTIN-DEPOLYMERIZING FACTOR/COFILIN (ADF/CFL) gene family. Plos One, 10(12), e0145917. doi:10.1371/journal.pone.0145917

Satir, P. (2016). Chirality of the cytoskeleton in the origins of cellular asymmetry. Philosophical Transactions of the Royal Society Biological Science, 371, 20150408 http://dx.doi.org/10.1098/rstb.2015.0408

Scharff, C., and Petri, J. (2011). Evo-devo, deep homology and FoxP2: implications for the evolution of speech and language. Philosophical Transactions of the Royal Society Biological Science, 366, 2124-2140. doi:10.1098/rstb.2011.0001

Siccardi, E., and Adamatzky, A. (2016), Quantum actin automata and three-valued logics. IEEE Journal of Emerging and Selected Topics in Circuits and Systems, Doi: 10.1109/JETCAS.2016.2528722.

Sluder, G. (2014). One to only two: a short history of the centrosome and its duplication. Philosophical Transactions of the Royal Society Biological Science, 369, 20130455. http://dx.doi.org/10.1098/rstb.2013.0455

Smouse, PE., Focardi, S., Moorcroft, PR., Kie, JG., Forester, JD., and Morales, JM. (2010). Stochastic modelling of animal movement. Philosophical Transactions of the Royal Society Biological Science, 365, 2201–2211 doi:10.1098/rstb.2010.0078

Sousa, FL., Thiergart, T., Landan, G., Nelson-Sathi, S., Pereira, IAC., Allen, JF., Lane, N., and Martin,WF. (2013). Early bioenergetic evolution. Philosophical Transactions of the Royal Society Biological Science, 368, 20130088. http://dx.doi.org/10.1098/rstb.2013.0088

Stairs, CW., Leger, MM., and Roger, A. (2015). Diversity and origins of anaerobic metabolism in mitochondria and related organelles. Philosophical Transactions of the Royal Society Biological Science, 370, 20140326.http://dx.doi.org/10.1098/rstb.2014.0326

Stout, D., and Chaminade, T. (2012). Stone tools, language and the brain in human evolution. Philosophical Transactions of the Royal Society Biological Science, 367, 75–87 doi:10.1098/rstb.2011.0099

Strausfeld, NJ., and Hirth, F. (2016). Introduction to "homology and convergence in nervous system evolution". Philosophical Transactions of the Royal Society Biological Science, 371, 20150034. http://dx.doi.org/10.1098/rstb.2015.0034

Taylor, SS., Keshwani, MM., Steichen, JM., and Kornev, AP. (2012). Evolution of the eukaryotic protein kinases as dynamic molecular switches. Philosophical Transactions of the Royal Society Biological Science, 367, 2517–2528. doi:10.1098/rstb.2012.0054

Tekle, YI., and Williams, JR. (2016). Cytoskeletal architecture and its evolutionary significance in amoeboid eukaryotes and their mode locomotion. Philosophical Transactions of the Royal Society Biological Science, 3, 160283. http://dx.doi.org/10.1098/rsos.160283

Thauer, RK., Kaster, AK., Seedorf, H., Buckel, W., & Hedderich, R. (2008). Methanogenic archaea: ecological relevant differences in energy conservation. Nature Reviews Microbiology, 6, 579-591.

Thomas, C., and Staiger, C. (2014). A dynamic interplay between membranes and the cytoskeleton critical for cell development and signaling. Frontiers in Plant Science, doi: 10.3389/fpls.2014.00335.

Van den Ent, F., Amos, LA., Löwe, J. (2001). Prokaryotic origin of the actin cytoskeleton. Nature, 413, 39-44, doi:10.1038/35092500

Venticinque, L., Jamieson, KV., Meruelo, D. (2011). Interactions between lamina receptor and the cytoskeleton during translation a cell motility. Plos One, 6(1), e15895. doi:10.1371/journal.pone.0015895

ORIGINALES / ORIGINAL PAPERS

Wickstead, B., and Gull, K. (2011). The evolution of the cytoskeleton. The Journal of Cell Biology, 194(4), 513-525. www.jcb.org/cgi/doi/10.1083/jcb.201102065

Yi, Z., Huang, L., Yang, R., Lin, X., Song, W. (2016). Actin evolution in ciliates (Protist, Alveolata) is characterized by high diversity and three duplication events. Molecular Phylogenetics and Evolution, 96, 45-54

Zhu, L., Zhang, Y., Hu, Y., Wen, T., and Wang, Q. (2013). Dynamic actin gene family evolution in primates. Biomedical Research International, http://dx.doi.org/10.1155/2013/630803