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A Sequential Scenario for the Origin of Biological Chirality

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Abstract. A sequential model is proposed regarding the origin of biological chirality. Three major stages are presumed: a symmetry breaking (prebiotic chiral disruption in enantiomeric mixtures of monomers), a chiral amplification (prebiotic increase of the chiral character of the monomers affected first by the symmetry breaking), and a chiral expansion (proto biological increase of the chiral character and spread of the chirality to molecules which were less affected by prebiotic chiralizations). As a symmetry-breaking mechanism, the model proposed by Deutsch (1991) is used, which involves a dissymmetric exposure of amino acids (AA) to ultraviolet circularly polarized light (UV-CPL) on evaporative seashores. It is presumed that the chiral amplification, up to a protobiologic significance, was influenced by a periodic overlapping of two abiotic events, a synchronization between tidal-based hydrous–anhydrous cycles, and littoral asymmetric photolysis cycles. This long-term astronomic asymmetry acted around 3.8–4.2 billion years ago and was unique to the Earth in our solar system. It is also presumed that the abiotic symmetry breaking is heterogenous, that only a few L-AAs were used in the beginning, and that the chirality expanded later to all 20 AAs based on a coevolutionary strategy of the genetic code and on a physiological relationship between AAs. In this scenario the D-chirality of pentoses in polynucleotides was attributed to both D-pentose/L-AA relationships and to a structural evolution.

Key words: Origin — Chiral — Handedness — Amino acid — Moon — Tides — Coevolution

Introduction

The living world exhibits a very conservative chirality. Only L-AAs (L amino acids) exist in proteins and only D-sugars in nucleic acids. This asymmetry is essential in the living world for (1) creation of conformational patterns, (2) control of the spatial orientation of radicals, and (3) controlling folding patterns. The consistency of the symmetry violation in the living world suggests an archaic character (Thiemann and Teutsch 1990). Since the first forms of life were too simple to control the chirality it is commonly supposed that the chirality was initiated (and amplified) by abiotic factors (Goldanskii and Kuzmin 1991). Most hypotheses regarding the origin of biological handedness tried to identify disruptions in the natural symmetry which initiate the prebiotic chirality. So far, none of these hypotheses has adequately described a comprehensive scenario regarding the emergence of biological handedness. These hypotheses have been limited because of the modest results of the abiotic symmetry breaking, and the lack of knowledge regarding the protobiological evolutionary pathways.

The hypothesis presented in this paper is based on four postulates:

1. The biogenetic environment was a subaerial aqueous milieu.
2. Modern biochemical handedness is not the result of a singular mechanism but the result of a succession of abiotic and protobiological events.
3. An abiotic chiral amplification occurred after a natural symmetry breaking, based on a periodic asymmetry which acted in the biogenetic environment.
4. The biological expansion of the chirality was driven by selective advantages and was the result of an evo-

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lutionary process contemporaneous (and related) with the maturation of the genetic code.

Regarding the biogenetic environment, it has already been suggested that life could emerge in subaerial microspaces such as basaltic lava littoral surfaces (Fox 1964), clay minerals (Cairns-Smith and Hartman 1986), lagoons, evaporative shores, littoral hydrothermal hot spots, tidal pools (Horgan 1991), littoral sediments (Glover 1992), and pyrite surfaces (Wächtershäuser 1988). Since the paleotides were very high most of these environments were affected twice daily by hydrous–anhydrous cycles. I agree that the chiral amplification was related to tidal patterns. The Moon was close to the Earth, and the tides were very high, covering large surfaces. Since the sideral month was very short, for some long periods of time the sideral month was an integer divisor of the Earth's rotational period. Consequently a periodic asymmetrical pattern resulted. The tidal flooding overlapped with the nictemeral cycles. The symmetry in the monomers' exposure to UV-CPL was consistently violated. In some intertidal areas and for some periods of time an excess of L-AA or D-AA appeared, increasing abiotic chirality. The first forms of life initiated prebiological evolution using the enriched chiral mixtures. The expansion of the chirality to all AAs, as well as to the nucleotidic pentoses, was controlled primarily by a coevolutive scenario in the maturation of the genetic code and by the L-AA/D-ribose relationship.

The Symmetry Breaking

Many natural factors are presumed to have been responsible for the initiation of the chirality in AAs (Thiemann 1975; Lacey et al. 1993): an L-stabilization of some AAs (e.g., Ala, Val, Ser, Asp) relative to the D forms (Salam 1991), an increase in the efficiency of photo resolution in the presence of minerals containing Cr^{3+} (Norden 1977), a stereospecific absorption on kaolin (Flores and Bonner 1974), stereospecific interactions with quartz crystals (Palache et al. 1962; Furuyama et al. 1982), metal complexes acting as prenucleoprotic mediators of a molecular asymmetry (Decker 1975); a parity violation in weak interactions (Kondepudi and Nelson 1985), interactions with β-particles (Garay 1968; Garay et al. 1973; Kovacs 1979), specific interactions between D-pentoses and L-AA (Yarus 1988), inhibition of the spontaneous racemization induced by $D \rightleftarrows L$ tunneling (predicted by Hund's paradox) at temperatures still compatible with cryochemical reactions (Goldanskii and Kuzmin 1991), and asymmetric growth of crystal structures under the influence of light or the Earth's magnetic field (Thiemann and Teutsch 1990).

Since this model is based on the presumption of a subsurface environment and of a tidal-photolysis pattern, I used the stereo-selective photochemical destruction with ultraviolet circularly polarized light (UV-CPL) (Mörtberg 1971; Deutsch 1991), as a prebiotic symmetry breaking mechanism. Part of the UV light (about 0.4%) is circularly polarized (Wolstencroft 1985), with a light dominance of left circularly polarized light (LCPL) in the mornings (sunrise) vs a dominance of right circularly polarized light (RCPL) in the afternoons (sunset) (Angel et al. 1972). The asymmetric circular polarization is a result of either the influence of the terrestrial magnetic field on the UV polarized light, reflections on the Earth's surface (Kagan et al. 1974; Flores et al. 1977), or successive refractions in the atmosphere (Mortberg 1971; Balavoine et al. 1974). The AAs which were exposed to light on archaic seashores after evaporative cycles, were subjected to a nonsymmetrical UV-CPL photolysis. R-leucine is degraded more rapidly in the presence of UV-RCPL (and vice versa for L-leucine), (Flores et al. 1977). The measured preference of RCPL for asymmetric photolysis of D-AA was about 2% (Flores et al. 1977). This phenomenon was also verified for Ala and Glu. UV-CPL–induced chirality is based more on a stereo-selective photochemical destruction than on a photo conversion (Thiemann 1975); therefore it is primarily determined by the circular dichroism (CD). Other AAs may be also stero selected in the same fashion since ''the α-AA of L-configuration show a positive Cotton effect around 215 nm, while their D-enantiomers display a Cotton effect of an opposite sign'' (Crabbé 1965). Since UV-RCPL photolyses more D-AA, and since more UV-LCPL appears in the morning (and more UV-RCPL in the afternoons), it was presumed that a light excess of D-AA could appear in the archaic mornings and an excess of L-AA in the afternoons (Kagan et al. 1974).

The Chiral Amplification

The natural chirality resulting each day from the daily UV-CPL asymmetric photolysis was probably very small. Some long-term asymmetric factors probably reiterated the effect of the chiral breaking and eventually created enriched chiral mxitures. Some mechanisms enhancing (or at least maintaining) the initial chirality have been proposed: A tendency of the stereoisomers to bind to the same optic form during abiotic condensations (Mason 1988; Thiemann 1975) and a competition between enantiomers after a spontaneous symmetry breaking (an increased stability of the oligomers built up from optically pure monomers as compared with those built up from racemic mixtures (Blout and Idelson 1956; Harada and Matsumoto 1970). Some models attempted to explain the increase in the importance of L-AA. Increased stability was observed in α-helixes and β-sheets made up from L-AA compared with same structures based on D-AA (Mason and Tranter 1984; Tranter 1985). Deutsch (1991) referred to differences regarding the average temperatures between mornings and afternoons. The amount of L-AA photolyzed in the morning was less than the amount of D-AA photolyzed in the afternoon (Deutsch

1991). If this mechanism was repeated ‘‘day after day’’ a ‘‘substantial different in the ultimate ratio of R to S forms of chiral compounds’’ appeared (Deutsch 1991). It was experimentally demonstrated that after 7–500 h of irradiation of AA with UV-CPL, an enantiomeric excess of 0.06–2.5% L-AA appeared (Norden 1977).

I propose two possible mechanisms for the chiral amplification related with symmetry breaking via UV-CPL asymmetric photolysis: (1) periodicity in UV-CPL photolysis created by lunar synchronous tides and (2) influence of the lunar magnetic field.

Periodicity in UV-CPL Photolysis Created by Lunar Synchronous Tides

A ‘‘long-term’’ astronomical asymmetry exists on Earth. A single satellite (with a posigrade orbit) exists which is one of the biggest satellites in our solar system (1/80th the Earth’s mass). (The only other planet with a single satellite is Pluto, which is too cold and small to have liquid water on the surface and tides affecting a hydrosphere. On the archaic Earth, the geographic areas most affected by tidal dehydration cycles and by UV exposure were the intertidal surfaces and the subjacent micro spaces.)

I propose that if a synchronization existed between the tidal cycles and the photolytic cycles an accumulation of chiral components could occur. If one analyzes the patterns created by the solar tides, a synchronization existed between the tidal flooding and the photolytic cycles. But, if the Moon existed 4 billion years ago, the solar tides would not have much importance. Some data support an age of the Moon between 4 and 4.5 billion years ago (Chaisson and McMillan 1993). For a planet with a peculiar geo-astronomical conjuncture like the archaic Earth, with a big Moon close to the planet (Kaula and Harris 1973), a planetary-spread ocean with a rather flat relief, and relatively short days, the archaic paleotides were enormous (up to 1–2 km) (Goldreich 1972) and frequent (every few hours). The Moon probably assisted in the emergence of life on Earth because it is more than 4 billion years old (Chaisson and McMillan 1993). Considering the emergence of life in littoral areas, the importance of the paleotides cannot be neglected. Some data regarding the lunar orbit support this scenario. Four billion years ago, the Earth rotated fast (>5 h), (Goldreich 1972), the Moon was very close to the Roche limit (2.86–10 Earth radii), and the sideral month was very short (>6.76 h), (Kaula and Harris 1973; Kaula 1993, personal communication). The evolution of the sideral month is depicted in Fig. 1. The ancient proximity of the Moon was deduced from measurements of the lunar equatorial bulge (Chaisson and McMillan 1993), of the growth speed of stromatolites (Mohr 1975; Pertunen 1970), of corals (Wells 1966), and of growth bands on Nautiloid shells (Kahn and Pompea 1978).

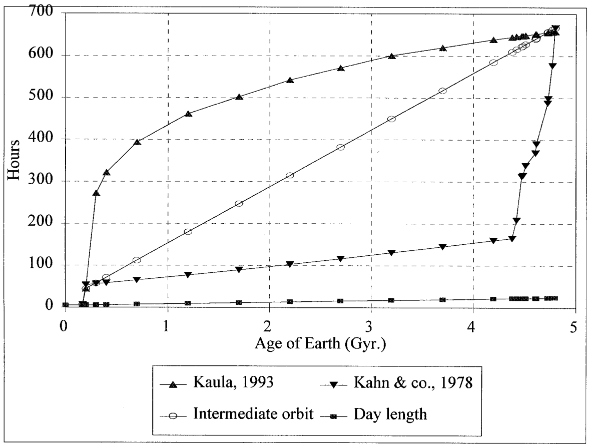

Fig. 1. The hypothetical evolution of the sideral month in geological periods. Unavailable values and intermediate orbit were obtained from linear interpolation assuming an initial orbit of the Moon at the Roche limit and an age of 4.5 billion years (Gyr).

Contemporaneous lunar tides are asynchronous (cannot create a tidal-photolytic pattern), but by analyzing the orbital characteristics of the Moon in the past, one notices that periods with lunar synchronous tides have existed. (The tidal synchronism is defined as the situation when the orbital period of the moon—the sideral month—was a multiple integer of half of the day.) After a constant and small number of days the Moon passed over the same meridian at the same hour. The tidal cycles overlapped with the asymmetric photolysis cycles, and in a long period this effect became significant. After each flooding cycle, chiral mixtures of AA probably infiltrated in the subsurface aquifers.

The ratio between the sideral month and the day was small (Kahn and Pompea 1978), but it is still questionable whether a 1:1 synchronism existed or not (Kaula and Harris 1973). However, 2:1, 2.5:1, 3:1, 3.5:1, etc., synchronisms probably existed since the initial month: day ratio was close to 1 (Kaula and Harris 1975) and is currently around 27.3:1. The periods with synchronous tides were more frequent in the past (Fig. 2) because the days as well as the sideral months were so short and also because the sideral month increased faster than the day. The length of the synchronous periods can be estimated by how slowly the sideral months changed (Fig. 4). Figure 4 shows a very slow change of the sideral month (max 1 s in 1000 years).

The necessary period for the tidal synchronism to have a planetary impact on the chirality is difficult to estimate since it depended on many factors, such as intensity of UV irradiation, amplitude of UV photochemical destruction, level of circular polarization of UV light, difference between LCPL and RCPL, preference for homochiral destruction, temperature, AA racemization, surface exposed each day to tidal denudation, the ocean volume, etc. However, in restricted areas, like littoral subsurfaces, the effect must have been greater and de-

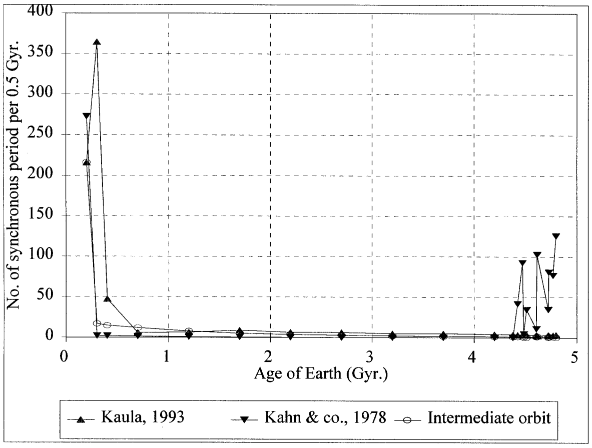

Fig. 2. Frequency of periods with synchronous tides in the Earth's history (= F). Derived from calculations for different orbits of the Moon.

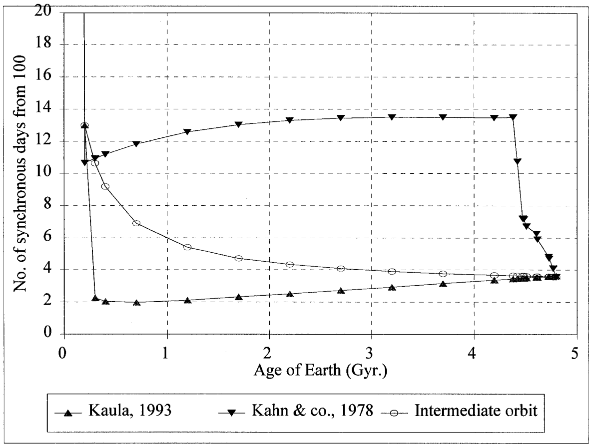

Fig. 3. Occurrence of the synchronous days in different geological periods (= R). The graph describes the frequency of days with synchronous tides (from 100) in a given synchronous situation, derived from calculations for different orbits of the Moon.

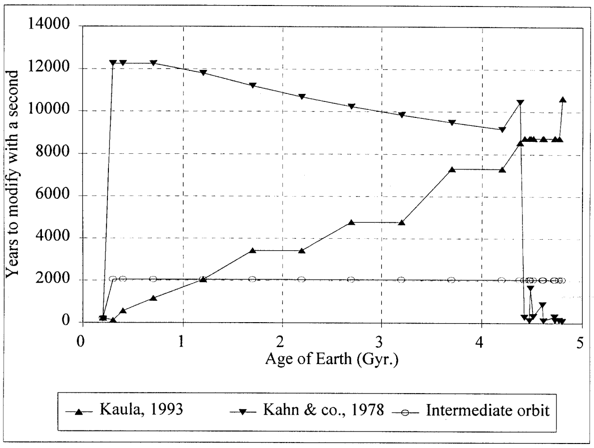

Fig. 4. Relative length of synchronous periods in different geological periods (= T). The graph describes how many years were necessary for the sideral month to increase by 1 s. Derived from calculations for different orbits of the Moon.

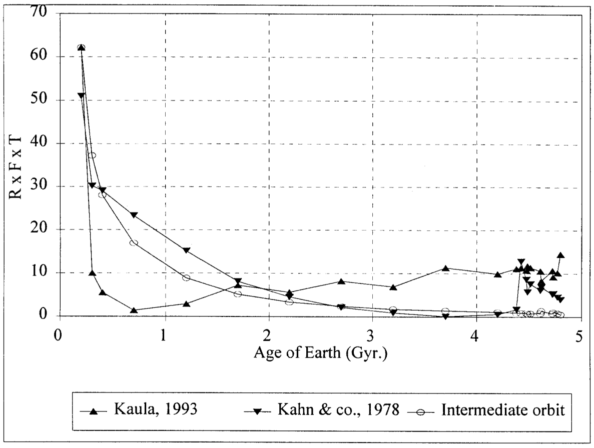

Fig. 5. The importance of the synchronous tides in chiral amplification for different possible lunar dynamics. The relative effect in different geological periods was estimated as a function of F, R, and T (Figs. 2–4).

pended on the redundancy of the process. Considering an archaic year of about 1,400 days (each one of 6 h), for 10,000 years (the period during which the sideral month changed by less than 20 s), (Fig. 4), and given a 2:1 ratio between sideral month and day, the asymmetric photolysis cycles repeated every 6 h almost 10,000,000 times.

The importance of the lunar synchronism for the accumulation of optic isomers in different geological periods depended on three main factors: the frequency of the periods with synchronous tides (F) (Fig. 2); the frequency of synchronous days in given synchronous periods (R) (Fig. 3), and the length of the synchronous periods (T) (Fig. 4). As observed in Fig. 5 the influence of synchronous tides on enhancing the chirality was high in the very first period of the Earth–Moon relationship. Figure 5 also suggests that regardless of the lunar orbit (e.g., Kaula scenario, Kahn and Pompea scenario, or an intermediate scenario), the effect induced by the synchronous tides was very high in the very beginning and later decreased. Considering 4.0–4.5 billion years as an estimated age of the Moon, the period with the greatest probability for lunar-driven accumulation of chirals occurred around 3.9–4.4 billion years ago. This period corresponds with the time when life arose on Earth (around 4 billion years ago). Accordingly, we consider that the Moon could influence the emergence of life on Earth through peculiar orbital characteristics.

The Influence of the Lunar Magnetic Field

Some experiments indicated an influence of the magnetic fields on the chiral syntheses. The Earth's magnetic field affected the chirality of the archaic oligomers (Bradley 1994). Another magnetic distortion could have been produced by the Moon. Today, the lunar magnetic field is

Table 1. Evolutionary scenario for the origin of biological chirality in AA

Step No.	Evolutionary stage	Mechanism	Effect
1	Abiotic chiralization	Asymmetric photolysis with UV-CPL light	Initiation of chirality (symmetry breaking)
2		Lunar synchronous tides	Redundance of symmetry breaking. (amplification of initial chirality)
3		Influence of the lunar magnetic field.	Possible light enhancement of chirality
4	Protobiological chiralization	Selection for structural stability	Enhancing chirality for each AA
5		Biosynthetic relationship between AAs	Expanding chirality to all 20 AAs
6		Phylogenetic relationship between AA-tRNA-Syn	

not significant because the Moon is far from the Earth and its core is no longer melted. It has been presumed that the Moon was partially melted 4 billion years ago because the lunar maria solidified around 3 billion years ago (Chaisson 1988). If the lunar magnetism was stronger and the tidal synchronization existed, the lunar magnetic field could have been synchronous with dehydrous (condensing) cycles. However, there is not enough supporting data for this hypothesis.

The Chiral Expansion

The level as asymmetric photolysis is different for each monomer because significant differences exist in the intensity of CD depending on the conformation and the absolute configuration (Crabbé 1965). Enriched chiral mixtures could have appeared but the natural mechanisms alone could not generate and maintain the level of chiral purity required for proteic AA. Most likely the first forms of life began by using enriched chiral mixtures and only few monomers, and evolutionary mechanisms perfected later the chirality. The protobiological perfection of chirality probably acted in two directions: improving the level of chirality of each monomer (Thiemann and Teutsch 1990) and expanding the chirality to other monomers.

Improving the Level of Chirality of Each AA Was Directed by a Structural Evolution

Optically pure polymers (e.g., poly-AAs) are more stable than the racemic polymers (Harada and Matsumoto 1970), causing an asymmetry which offered a selective advantage both in chemical and biochemical evolution (Kovacs 1979). The structure of the genetic code suggested that the control of hydrophobic–hydrophilic relationships and the polarity of AA were particularly important during early evolution (Goldman 1993). Since chirality controls the geometrical patterns of macro molecules (Hegstrom and Kondepudi 1990), it was considered that selection occurred, intensifying the initial chirality (Thiemann and Teutsch 1990).

The Expansion of L-Chirality to all AAs Was Directed by a Coevolution

Recent developments in biochemistry and molecular biology have allowed a clearer image regarding the structure of the components involved in translation. The genetic code was not as complex as it is now. The archaic codes were probably less precise (Goldman 1993) and very simple, using fewer AAs and fewer nitrogenous bases (Hartman 1984). This may have led to the erroneous assumption that protocells remained captive in an L-AA rich environment until they assimilated all 20 AAs as L-forms. It is more likely that some AAs were added later (Wong and Broskill 1979) and that selective factors acted during the maturation of the genetic code, expanding the use of L-stereoisomers to all 20 AAs.

This assumption is supported by the following data:

1. The phylogeny of tRNA is correlated with the biosynthetic distances between AAs (Di Giulio 1994). This observation is in accordance with the ‘‘coevolution hypothesis’’ (Wong 1975), which explains a coevolution between the biosynthetic neighborhoods of the AA and the organization of the genetic code. Probably only a few AAs were used at the very beginning (e.g., Ala, Arg, Pro) (Hartman 1978), while the others were synthesized later, using the first group as a starting point. If the code started with a few L-AAs and if the other AAs derived metabolically one from each other, then the L-asymmetric carbons could have been used as building blocks and eventually all AAs would have been L-stereoisomers.
2. Studying the phylogeny of the aminoacyl tRNA synthetases (AA-tRNA-Syn) the ‘‘coevolution hypothesis’’ was found the most probable scenario for the maturation of the genetic code (Di Giulio 1992). Each AA-tRNA-Syn offers specific sites for binding specific AAs (Stryer 1988) (e.g., the asymmetric carbon of the Tyr is surrounded by no less than six hydrogen bonds). This spatial architecture allows a high specificity for AA recognition. It also allows the precise identification of the L-form. Since the spatial architecture of the site binding the AA is a conservative

> attribute, chances are an AA-tRNA-Syn binding an L-AA would evolve into another AA-tRNA-Syn which also recognized and L-AA. These two mechanisms could eventually lead to the expansion of L-asymmetry expansion to all AAs.

Conclusions

This proposal suggests that L-AA accumulated in intertidal subterranean microspaces. Chirality was abiotically initiated. A peculiar astronomical context almost 4 billion years ago which produced tides synchronized with the littoral photolysis and condensing cycles synchronized with fluctuations of the magnetic field resulted in chiral mixtures of AAs which accumulated on seashores and infiltrated in porous aquifers (Table 1). Protobiological mechanisms like a selection for nonrandomness in proteic structures, biosynthetic relationships between AAs, and the phylogenetic inheritance of the geometry of the AA binding site from the AA-tRNA-Syn extended the L-chirality to its present state.

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