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Collective Memory and the Hologenome Concept

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Collective Memory and the Hologenome Concept

Stephanie Rotem [α] & Eugene Rosenberg [σ]

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I. Introduction

During the last few years, fundamental changes have taken place in our understanding of biology, which may be relevant to the concept of collective memory. In particular, it is now clear that all animals, including humans, contain abundant and diverse symbiotic microbes that play an important role in their adaptation, behavior and evolution. The fact that these microbial populations are dynamic and their vast genetic information can change as a function of the environment makes it possible for them particularly well-suited to acquire and store DNA-based memory. Furthermore, these changes in microbial DNA can be transferred horizontally to other members of the community and vertically to offspring. How these symbiotic microbes contribute to certain aspects of collective memory is the subject of this article.

The term "Collective Memory" is widely used in articles in history and sociology. Collective memory discourse began with the work of Emile Durkheim (1858–1917), a French philosopher, sociologist and social psychologist. Although never using the term "collective memory", Durkheim noted that societies require continuity and connection with the past to preserve social unity and cohesion. Maurice Halbwachs (1877–1945), a student of Durkheim, is the first sociologist to use the term "collective memory" and his work is considered the foundational framework for the study of societal remembrance (Halbwachs, 1980). Halbwachs suggested that all individual memory was constructed within social structures and institutions and claimed that individual private memory is understood only through a group context; these groups may include families, organizations, and nation-states. Cultural or social memory is the specific character that a person derives from belonging to a distinct society and culture as a result of socialization and customs (Assmann, 2003).

Carl Jung (1876-1961) used the term "collective unconscious" to describe the broad concept of inherited traits, intuitions and collective wisdom of the past. The collective unconscious, unlike the personal unconscious, is a type of genetic memory that can be shared by individuals with a common ancestor or history. According to Jung, the collective unconscious consists of implicit beliefs and thoughts held by our ancestors (Lu 2012). While we are not aware of the collective unconscious, it can influence how we act. What Jung termed the collective unconscious or genetic memory may now be referred to as DNA-based memory (Bullock andStallybrass1977).

During the last twenty years, new techniques of analyzing DNA have fundamentally changed our understanding of biology (Douglas, 2010). Animals, including humans, can no longer be considered individuals by the classical definitions of the term. All are holobionts, or collectives, consisting of the host and abundant and diverse symbiotic microorganisms (Zilber-Rosenberg and Rosenberg 2008; Rosenberg and Zilber-Rosenberg 2014). Symbiosis—once thought to be a peripheral phenomenon—is the hallmark of life on earth (Gordon, 2012). After reviewing our current understanding of the role of microorganisms in the fitness and evolution of multicellular organisms, we will examine the similarities and differences of collective memory as exhibited by the human genome, the human microbial DNA and cultures, as well as their interactions.

Since certain specialized terms are used throughout this article, we would like to define these terms before discussing the concepts. Symbiosis (from Greek σύν "together" and βίωσις "living") is the close and often long-term interaction between two or more

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different biological species. The term holobiont, introduced by Margulis (1991), describes a host animal or plant and all of its symbiotic microorganisms, including Bacteria, Archaea, fungi, algae and viruses. The term "host" is used here in the classical sense to denote the larger, multicellular organism in or on which the symbionts reside. Zilber-Rosenberg and Rosenberg (2008) introduced the term hologenome to describe the sum of the genetic information of the host and its symbiotic microor-ganisms. The aggregate of all microorganisms of a holobiont is known as the microbiota or microbiome, a term coined by Lederberg and McCray (2001).

II. The Hologenome Concept

We are in the midst of a paradigm change in biology. Numerous studies have demonstrated that all animals and plants contain abundant and diverse microbiota. The human body, for example, contains about the same number of microbial cells as human cells (Rosner, 2014).Because the microbial community is composed of several thousand different species of bacteria, the genetic information encoded in the microbiome (eight million unique genes)is more than 400times greater than the information in the human genome (19,000 genes) (Ezkurdia et al., 2014). The microbial symbionts contribute to the anatomy, physiology, development, innate and adaptive immunity, behavior, genetic variation and evolution of holobionts (Zilber-Rosenberg and Rosenberg 2008; Round et al., 2010; Gilbert et al., 2012; McFall-Ngai et al., 2013). As we shall reveal in this article, the DNA of the microbiota in addition to the human genome contributes to collective memory.

Microbial symbionts can be transmitted with fidelity from parent to offspring by a variety of methods, including cytoplasmic inheritance, coprophagy (consumption of feces), direct contact during and after birth, and via the environment (Rosenberg and Zilber-Rosenberg 2014). In humans, most of the colonization of the newborn gut occurs when the baby transits the birth canal via inoculation by maternal vaginal and fecal microbes. Furthermore, human breast milk has been shown to be a continuous source of bacteria to the infant gut (Fernández et al., 2013). The hologenome concept of evolution posits that the holobiont (host + symbionts) with its hologenome (host genome + microbiome) is an important unit of selection in evolution (Zilber-Rosenberg and Rosenberg 2008). Consideration of the holobiont as a unit of selection brings forth previously under-appreciated patterns of genetic variation (changes in the hologenome). In fact, acquisition of microbes and microbial genes is a powerful mechanism for driving the origin of species and evolution of complexity. In essence, holobionts are collectives and evolution proceeds both via cooperation and competition, going hand in hand.

In considering the role of DNA in collective memory, it is necessary to separate the hologenome into two parts: (i) the human genome, which consists of 19,000 genes located on the 23 pairs of chromosomes, and (ii) the human microbial genes, which consists of 8,000,000 genes and is present in the thousands of different species of microbial symbionts, mostly in our gut. Genetic variation in the human genome results from mutations, which are random events that occur rarely. Genetic variation in the human microbiome, however, can occur rapidly in response to changes in the environment (Rosenberg and Zilber-Rosenberg 2016). Accordingly, the microbiome is particularly well-suited to serve as a vehicle for DNA-based collective memory.

III. Acquisition of Collective Memory via Culture and dna

Both cultural and DNA-based memories can be gained or lost. Acquisition of collective memory requires a shared experience and the deposition of the experience in a manner that can be recalled at a later time (Gintis, 2011). An example of a recent cultural memory is the Holocaust, a genocide in which approximately six million Jews and five million non-Jews were killed by Adolf Hitler's Nazi regime and its collaborators.The Holocaust experience has been documented in personal accounts, historical writings, films and museums. In addition, an annual International Holocaust Remembrance Day is observed. As is often the case, different groups share divergent versions of the event, as is evident from the foci of various National Holocaust Museums (Rotem, 2013).

A classic example of host gene-culture coevolution is the consumption and digestion of milk. A major source of carbon and energy in milk is the disaccharide lactose. For lactose to be utilized, it must first be split into monosaccharides by the enzyme lactase. The enzyme is abundant in infants, but the activity of the enzyme is dramatically reduced after weaning (Swallow, 2003). When adult humans first began consuming milk and milk products from domesticated animals in central Europe approximately 10,000 years ago, they could not digest lactose. Genes that allowed for the digestion of lactose, referred to as lactase persistence genes (Gerbault, 2011), evolved and eventually spread among milk-drinking peoples. Current estimates for the age of lactase persistence-associated alleles bracket those for the origins of animal domestication and the culturally transmitted practice of dairying. Cultures that traditionally do not consume milk products, such as Australian Aborigines, Japanese, and Native Americans, have extremely high rates of lactose intolerance. There are many examples of cultural practice driving human evolution (Rowley-Conway and Layton 2011) but none are so well studied, clear-cut, widespread and well supported as the coevolution of

lactase persistence and dairying (Holden and Mace 1997).

In European populations, a single mutation explains the distribution of the lactose persistence phenotype, whereas different point mutations are associated with it in Africa and the Middle East. It should be pointed out that the mutation does not result in a novel lactase but ratherin an enhancer region of the existing lactase gene (Harvey, 1995). Lactose persistence is readily explained by Neo-Darwinian variation by mutation followed by Darwinian selection. As we shall discuss below not all gene variation results from mutation of the human genome and not all cultural evolution involves individual selection.

As an example of collective memory that is DNA-based but did arise from mutation of the human genome consider the use of agar in Japanese cuisine. Agar is a complex polysaccharide found in seaweed, which forms the supporting structure in the cell walls of certain species of algae. Throughout history into modern times, agar has been used as a food ingredient in Japan and throughout Asia. Foods that contain agar include wagashi, a dessert made of small cubes of agar jelly, mizuyōkan, another popular Japanese food, and sushi. The techniques for preparing these foods have been passed down from generation to generation and constitute part of the Japanese cultural collective memory. Tax records from the eighth century list seaweed as payment to the Japanese government, showing that it had an important role in Japanese culture (Nisizawa et al., 1987).

Interestingly, the Japanese also have acquired and retained in their DNA the ability to digest agar, because they have a bacterium in their gut that contains a gene that codes for the enzyme agarase (an enzyme that breaks down agar). Westerners lack this bacterium and cannot digest agar. The question then arises of how the agarase gene was acquired by the Japanese gut bacteria. The source of the gene was traced to a marine bacterium that was present on the dietary seaweed. However, this marine bacterium cannot survive in the human gut. DNA analysis showed that the agarose gene was horizontally transferred from the marine bacterium to a resident gut bacterium and became part of the hologenome of the Japanese (Hehemann et al., 2010).Until recently it was accepted that biological (DNA) memory was altered only by the random process of mutation. However, when considering the microbiota, it is clear that biological memory can also be changed by experience. When a person eats a particular food, those specific bacteria which can multiply on that food will amplify. At some later time when the person is again exposed to that food, the bacteria will rapidly degrade the food.

Each person possesses their own personalized fingerprint of gut microbiota (Faith et al., 2013), which includes a core microbiota of ca. 100 species which are common to all humans (part of the collective memory of the human species), hundreds of microbial species that are common to a particular culture (Yatsunenko et al. 2012), and thousands of microbial species that are present in a combination unique to each individual. Some strains of symbiotic bacteria are so well conserved within cultural groups that they can be used as a window into human migration (Yamaoka et al., 2009). In particular, the stomach bacterium *Helicobacter pylori* has been used as a marker of ancestry and migration (Dominguez-Bello and Blaser 2011). For example, an American whose great-great- grandmother came from Japan still contains the Japanese strain of *H. pylori*. The reduction of genetic diversity among humans as distance from East Africa is mirrored by the genetic distances between *H. pylori* strains circulating among human populations. Such parallelism is consistent with co-evolution of bacteria and their human hosts since their exodus from Africa.

Mice experiments have demonstrated that gut microbiota not only is involved in digestion of food but also affects the brain and behavior (Heijtz et al., 2011). Germ-free mice (born and grown under sterile conditions) are more active and spend more time scurrying around their enclosures than conventional mice. They are also less anxious and more likely to take risks, such as spending long periods of time in bright light or open spaces, compared to the normal mice. Inoculating the gut microbiota from healthy mice into germ-free baby mice caused them to behave in the "normal" cautious way. If sterile adult mice were inoculated with the gut bacteria, their behavior did not change, suggesting that the microbiota affect the early development of the brain that subsequently influences adult behavior (Foster and Neufeld 2013). There appears to be a critical window during development when the microbiota influence the central nervous system wiring related to stress-related behaviors. The data suggest that during evolution, the colonization of gut microbiota has become integrated into the programming of brain development, affecting motor control, anxiety-like behavior and probably many other behaviors.

How do gut bacteria affect the brain? To begin with, the long branching vagus nerve transmits information about what happens in the gut to the brain. But the bacteria also signal the brain via changing levels of dietary metabolites and hormones (Shaw, 2010). Hormones, by definition, can affect parts of the body over long distances. For example, blood plasma levels of the neurotransmitter serotonin were 2.8-fold higher in conventional mice than germ-free animals (Bercik et al., 2011). With regard to physical and psychological stress, the interaction of gut bacteria with the brain is bidirectional. Stress can affect the composition of intestinal microbiota, and as was discussed above commensal microbes affect the neural network

responsible for controlling stress responsiveness (Sudo et al., 2004).

Because learning about situations that are necessary for survival of a species is probably saved as a kind of unconscious genetic memory, some of these fundamental human experiences could be somewhere in our DNA. Consider that one of your ancestors had a very bad experience with fire. Such an experience, resulting in knowledge useful for survival, could possibly be encoded in the hologenome and passed on to future generations. In the fields of human genetics and microbiota so much is not known, especially regarding the functions of non-coding DNA (Mercer, 2009) that for an open-minded person, theories about deep DNA memories cannot be ruled-out.

IV. Loss of Collective Memory

Cultural and DNA-based collective memories can be lost if they are not used. Many languages have completely disappeared because of processes associated with colonization. For example, of the 250 Aboriginal languages that existed in Australia, only 60 remain (Amano, 2014), and of the more than 300 different languages that were spoken in North America when the Europeans first arrived, only 91 are still spoken (Braun, 2008). When a language becomes extinct, it can take along with it much of the history and culture of the people who spoke it.

DNA information can be lost by two general mechanisms: mutation and loss of microbiota. Mutation is a low frequency random event. If the mutation leads to the loss of a function, the mutation will be selected for if it benefits the organism. In the example we discussed above, a mutation in the gene that codes for agarase in the Japanese gut microbiota will be selected for if the Japanese person does not eat food that contains agar because the bacterium does not bear the burden of producing a useless enzyme. This is a very slow and inefficient method of changing DNA information.

Unlike chromosomal DNA, the microbiome is flexible and able to be easily modified to respond to altered circumstances or conditions, such as lifestyle and dietary patterns (Mueller et al., 2006).Changes in the microbiota, driven by the environment, can result in rapid gain or loss of DNA memory. Consider again the agar-digesting microbe in the Japanese gut. If seaweeds were removed from their diet, the microbe could not compete with other microbes in the gut and would soon be depleted, resulting in loss of the DNA memory to consume agar. In general, sustained alteration in the diet leads to gain or loss of certain microbes from the gut.

In modern Western cultures, microbes are lost as a result of improved sanitation and living conditions, overzealous antimicrobial therapy, delivery by caesarean section, and formula-feeding infants. All of these practices prevent acquisition of beneficial symbionts, which have evolved to participate in the metabolism and health of human holobionts. Loss of these beneficial microbes predisposes individuals to metabolic diseases (Blaser and Falkow 2009), susceptibility to allergic and autoimmune diseases (Penders et al., 2006), and may help explain the rise in obesity and related syndromes (Musso et al., 2010).

V. Jung's Theory of Collective Unconscious is Compatible with the Hologenome Concept

Like Freud, Jung emphasized the importance of the unconscious in relation to personality. However, Jung proposed that the unconscious consists of two layers (McLeod, 2014).The first layer called the personal unconscious is essentially the same as Freud's version of the unconscious. The personal unconscious contains temporality forgotten information and well as repressed memories. The second layer and the most important difference between Jung and Freud is Jung's concept of the collective unconscious. This is a level of unconscious shared with other members of the human species comprising latent memories from our ancestral and evolutionary past(Jung, 1953).Jung called these ancestral memories and archetypes.

Jung drew an analogy between instinct and archetype. The fact that instinctive behavior is a genetic (DNA) property of animal species is well documented (Tinbergen, 1951). It follows that DNA has the potential of being the reservoir of the archetypal symbols of the collective unconscious. The contentious question is how instinctual behavior and collective memory is obtained. According to Jung it was obtained by common experiences according to Lamarckian principles:

i. Use and disuse – individuals lose characteristics they do not use and develop characteristics that are useful.
ii. Inheritance of acquired characteristics – individuals transmit acquired characteristics to offspring.

Jean-Baptiste Lamarck, are nowned French botanist, zoologist and philosopher of science, published in 1809 his book *Philosophie Zoologique* (discussed in Burkhardt, 1972), describing environmentally induced changes that were then passed on to future generations. Interestingly, Darwin believed, as did Lamarck and many others at the time, that an organism can transmit traits it acquired during its lifetime to its offspring. But with the advent of Neo-Darwinism at the beginning of the 20thcentury, Lamarckism and, by association, Jung's concept of collective unconscious were discredited and largely ignored. There were two major scientific arguments for rejecting Lamarckism. First, the evolutionary theorist August Weismann argued that inheritance only takes place by means of germ cells

and that germ cells cannot be affected by anything somatic cells of the body acquire during their lifetime (Weismann, 1893). Second, Mendelian genetics considers that variation, the raw material for Darwinian evolution, occurs by random mutations in the population.

Since the 1980s, Lamarckism is being reconsidered with growing interest by mainstream evolution thought (Gould, 1999). It is now clear that environmental factors affect epigenetic inheritance systems that include DNA methylation, self-sustaining feedback loops, prions, chromatin-marking and RNA interference. Taken together these mechanisms include the inheritance of changes that are not DNA sequence based and therefore argue for withdrawal from the strict genotype–phenotype separation dogma of Neo-Darwinism (Jablonka and Lamb 2014).

Until recently it was accepted that biological (DNA) memory was altered by the random process of mutation of genes. However, consideration of the hologenome, namely the hostgenome combined with that of its microbiota, brings forth two additional modes of genetic variation which are specific to the holobiont and which conform to Lamarckism (Rosenberg et al., 2009). The first is microbial amplification, the increase of one group of microbial symbionts relative to others which can occur when conditions change. An increase in the number of a particular microbe is equivalent to gene amplification. Considering the large amount of genetic information encoded in the diverse microbial population of holobionts, microbial amplification can be a powerful mechanism for adapting to changing conditions. Examples of environmental factors that can lead to changes in the symbiont population and thereby tovariation in the hologenome are nutrient availability (Flint et al., 2007; Martens et al., 2008), temperature (Buddemeier et al., 2004; Koren and Rosenberg 2006), and antibiotics (de la Cruz and Davies 2005).

Another mechanism for introducing variation into holobionts is acquisition of new symbionts from the environment. Animals and plants come in contact with billions of microorganisms during their lifetime. It is reasonable to assume that occasionally, as a random event, some of these microbes will find a niche and become established in the host. Under the appropriate conditions, the novel symbionts may become more abundant and affect the phenotype of the holobiont. Unlike microbial amplification, acquiring new symbionts can introduce entirely new genes into the holobiont. Microbial amplification and acquisition of novel microbes into holobionts closely fit the Lamarckian first principle of 'use and disuse'. The holobiont loses characteristics (microbes) it does not use and gains characteristics (microbes) that are useful. These acquired microbes can be transmitted to off spring, thus satisfying the second principle of Lamarckism.

VI. Globalization and the Future of Collective Memory

Globalization refers to all those processes by which all the peoples of the world are incorporated into a single world society. Present media theorists sometimes link the notion of collective consciousness to signal the internet as a major intermediary in the creation of a truly global society. The Slovenian philosopher Slavoj Zizek described the consciousness of Internet culture as 'this neo-Jungian idea that we live in an age of mechanistic, false individualism and that we are now on the threshold of a new mutation. We all share a collective mind.'

Globalization is not limited to Internet usage, but takes many forms. Financial globalization is the integration of a country's local financial system with international financial markets and institutions. Large numbers of people are moving rapidly to distant locations, e.g., the recent mass migration of people from the Middle East and Africa to Europe. Food developed in one country soon becomes worldwide, e.g., coca cola and McDonald hamburgers. Similarly, sushi from the Far East is now consumed in the West. Globalization also has political, social, cultural and ideological aspects. It invades all aspects of our being, for better or for worse, in ways that were unimaginable only a few decades ago.

Collective memory is subject to both remembering and forgetting, suddenly and gradually (McBride, 2001).What we remember and what we forget is to a greater or lesser extent shaped by our social environment. The act of remembering goes on inside our heads but not independently of the social relations of which we are a part. Pieterse (2009) argues that globalization is a process of hybridization which gives rise to global mélange. For example, Pieterse explains how Turkish motifs were used in operas by Mozart, and American blues music reflects African Muslim origins. However, globalization is also a major contributing force in conflicts, such as the current violent confrontation between fundamental Islam and the West. In short, globalization results in numerous outcomes, including loss, gain and hybridization of collective memory and leads to both cooperation and competition.

Not only cultural memory but also DNA-based memory is affected by globalization. For example, the spread of Western diet and excessive hygienic practices has resulted in a loss of diversity in gut microbiota (Ley et al., 2008).The increasing role of industrial food in our alimentation is generating a globalization of our gut microbiota that may influence our health (Raoult, 2010). The increased movement of people and goods (part of globalization) has contributed to pandemics of infectious diseases caused by bacteria and viruses. It is also likely that there have also been pandemics of

beneficial microbes; however, they generally go unnoticed.

One of the dangers of globalization is loss of diversity, both cultural and DNA based. Biology has taught us that genetic diversity has a direct relation to the fitness and survivability of species and populations; as genetic diversity decreases within a population, so does the fitness and survivability of that population. Genetic diversity in human holobionts involves variability in the human genome and microbiome. Genetic diversity is important because the more variability there is within the species, the higher the likelihood that at least some of the individuals will be able to survive a major disturbance, such as a highly virulent emerging disease (Tishkoff and Verrelli2003). The same arguments can be made for cultural diversity. A diversity of cultures, expressing different visions of the world, provides a powerful resource for innovation (Nathan and Lee 2013), collaborative problem-solving (Page, 2008) and adaptation to a changing environment (Crisp and Turner 2011). In conclusion, based on the hologenome concept, we present for the first time the potential of the microbiome to serve as a vehicle for collective memory. This hypothesis is supported by the fact that the microbiome responds to the environment, that changes in the microbiome are transmitted to offspring and that behavior is influenced by the microbiome. What particular parts of the DNA-based collective memory resides in the human genome and the microbiota remains to be determined.

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