Gene and Meme

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PLEASE NOTE: This is a revised version of my chapter for the Encyclopedia of Animal Behavior. The earlier edition was published in 2019. This is a draft version which will have been edited before final publication. Do not quote from this version.

Key Points

Replicators and the evolutionary algorithm
Memes are a second replicator
Criticisms of memetics
Animal culture and imitation

Introduction

The word 'meme' was coined by Richard Dawkins' in his 1976 book *The Selfish Gene*. Although most people now associate memes with the notion of Internet memes, it is helpful to return to the original definition to understand the theory of memetics and its differences from other theories of cultural evolution.

The Selfish Gene popularised the gene's eye view of biological evolution. Yet, rather than confining his argument to selfish genes, Dawkins wanted to emphasise what he called 'universal Darwinism'. This is the general principle that whenever information is copied with variation and selection, evolution is inevitable. This process can be described as variation with selection and heredity, or as "blind variation with selective retention" (Campbell, 1960) although, as we shall see, the requirement for blind (or random) variation need not apply to all evolving systems. Dawkins distinguished between the information that is copied (the replicator), and the carrier of that information (the vehicle). This is similar to Hull's (1988) distinction between replicators and interactors. In the case of biology, genes are replicators and their phenotypes are their vehicles or interactors. Animals, in Dawkins' view, are the 'lumbering robots' that carry their replicators around and protect them.

The critical point is that these three steps: variation, selection and heredity, can be understood as a simple three-step algorithm, the evolutionary algorithm. This has been called 'Darwin's dangerous idea', a 'universal acid' that rips through all other explanations. "a scheme for creating Design out of Chaos without the aid of Mind." (Dennett 1995, 50). It was the generality of this scheme that Dawkins wanted to emphasise; 'Darwinism is too big a theory to be confined to the narrow context of the gene" (1976 p 191). He wanted "to claim almost limitless power for slightly inaccurate self-replicating entities, once they arise anywhere in the universe" (Dawkins 1989 p 322).

Genes may be replicators but they are only one example. In Dawkins' opinion, life anywhere in the universe would be driven by some kind of replicator, whether based on chemistry, electronic circuitry or anything else. This is why he asked, 'do we have to go to distant worlds to find other kinds of replicator and other, consequent, kinds of evolution?' and answered, 'no'. Staring us in the face is a second replicator, 'It is still in its infancy, still drifting clumsily about in its primeval soup … the soup of human culture' He wanted a name to convey the sense of a unit of imitation, and one that would rhyme with 'gene'. Taking, *mimeme* from the Greek meaning 'imitated thing' or 'that which is imitated', he chose the word 'meme'. Examples are 'tunes, ideas, catch-phrases, clothes fashions, ways of making pots or of building arches' (Dawkins 1976 p 192). We might add to his list, stories, poems, works of art, money, and much more. Memes group together into memeplexes whenever they can survive more effectively within the complex than alone. Memeplexes include religions and cults, conspiracy theories, financial institutions, and scientific theories, and much more. They depend on information being copied from person to person with variation and selection; they fit the idea of memes as replicator. In this way memetics echoes much earlier ideas, and indeed versions of universal Darwinism have a long history (e.g. Plotkin 1993, Campbell 2011).

In what sense then are replicators, whether genes or memes, selfish? *The Selfish Gene* popularised the view that biological evolution proceeds not for the benefit of the species or even the individual organism, but for the benefit of the underlying replicator. Dennett (1995), presses the important question '*Cui Bono?'* or 'Who benefits?' revealing the sense in which genes are 'selfish'. They will get copied whenever and however they can, regardless of the consequences to anything else; they, not the organisms or species, are the beneficiaries. This does not mean, as Dawkins pointed out over and over again, that the resulting organisms are selfish. Humans are just one of many species in which cooperation and altruism, as well as competition, have evolved from the underlying competition between genes.

Yet something else occurred during human evolution. Our ancestors, unlike other gene vehicles, became capable of imitating with high enough fidelity to give rise to a new replicator, the

meme, and consequently to cumulative cultural evolution. Memes are selfish in the same sense as genes are. They use human beings and their technology to get copied whenever they can regardless of the consequences; we are the meme machines that copy, vary and select memes (Blackmore 1999). We were the one species that let loose a second replicator with interests of its own. Memes can be either beneficial, neutral, or harmful to people and to human genes, but being beneficial is just one of many survival strategies for selfish memes.

There are significant differences between memetics and other theories of cultural evolution and they depend on this point. For memetics, memes are replicators that sustain a new evolutionary process operating on top of the old, and they evolve for their own benefit, not necessarily for the benefit of their carriers. For other theories of cultural evolution, such as gene-culture coevolution or dual-inheritance theory, cultural items are not replicators and the ultimate beneficiary remains genes.

This difference is illustrated by a close analysis of the horrific events of the medieval witch persecutions during which an estimated forty to fifty thousand 'witches', mostly but not exclusively women, were executed. A question that has long troubled historians is why these biased trials, cruel tortures, and killings continued for so long, and kept spreading in unstoppable waves, when they caused so much suffering. Suggestions included the changing climate and poverty, fears provoked by religious persecution, fear of the devil, or fear of women's boundless sexuality, or that someone, perhaps the clerics or the persecutors themselves, might have benefitted.

Applying a Darwinian analysis, Hofhuis and Boudry (2018, Boudry & Hofhuis, 2018) asked the critical question 'Who benefits?'. Studying the 'super-hunts' in the German city of Trier, they found that none of the usual explanations held water. The persecutors did not gain financially, the trials were time-consuming and expensive, and contemporary accounts show that the misery was suffered by everyone involved, harming individuals and tearing whole communities apart. They concluded that the cumulative concept of Western witchcraft with its beliefs in witches having pacts with the Devil and flying to Sabbats, was a form of socio-cultural design, apparently without designers, which did not substantially benefit any interested party. Asking which variants of witchcraft memes survived and why, they showed how it was possible for these memeplexes to grow and survive for their own benefit while harming the humans that made their spread possible.

Memes 'should be regarded as living structures, not just metaphorically but technically', writes Humphrey (in Dawkins, 1976 p 192). Rejecting memetics, Christiansen and Chater (2008) disagree. 'Following Darwin (1900), we argue that it is useful metaphorically to view languages as "organisms,"' (p 2). Yet in *The Descent of Man* (1871) Darwin does not call the analogies

metaphorical writing that, “The survival and preservation of certain favoured words in the struggle for existence is natural selection’ for both involve selection and modification with descent (Darwin 1871 p. 91). The proofs that both different languages and distinct species ‘have been developed through a gradual process, are curiously the same’ (Darwin 1871 p 59). In this way, Darwin’s view is closer to that of memetics than that of many modern critics.

Criticisms of memetics

Do memes even exist?

McGrath (2005) complains that there is “no direct evidence for the existence of ‘memes’ themselves” (p. 121), Aunger (2000) that “their existence has yet to be proven” (p. 7) and Wimsatt that they are “both misnamed and mischaracterized, and perhaps even that they do not exist” (1999 p. 280) or exist only if “conceptualised broadly and inclusively” (Wimsatt 2010 p 273). Yet, I would argue that even asking the existence question reveals misunderstanding of the original concept of memes (Blackmore 2010).

Do dollars exist? asks Dennett (2017). They seem to but this is only because dollar bills and coins exist; the ‘dollars’ themselves are essentially no different from bitcoins or other digital currencies. Do words exist? he asks. Of course they do, and words are the quintessential memes. There is no question about the existence of bicycles, phones, furniture, skyscrapers, tattoos, holiday brochures, cricket, or the days of the week. They are all information encoded in some kind of matter and energy, and all are sufficiently stable to either be copied or not. Since the core definition of memes is “that which is imitated”, all these examples count. Even if it is hard to pin down, whatever is copied is, by definition, a meme. So “the pertinent question is not whether memes exist, … but whether they are a useful theoretical expedient” (Laland & Odling-Smee, 2000). That is, whether thinking of words, stories, skills, habits and technologies as a new replicator is scientifically or philosophically useful. I say yes, many others say no. This, unlike the existence question, needs answering.

We may safely ignore the existence question and move on to more serious and productive questions. How helpful is the analogy with genes? What should and should not count as a meme? Are memes really replicators? Do they live inside brains, outside brains, or both, or are they purely abstract information? Above all, does memetics gives rise to any useful theoretical or practical progress?

Analogies, units, and other confusions

The idea that memes are analogous with genes has fuelled many objections, but these often miss the point and create unnecessary confusion. Midgley calls the idea ‘an empty and misleading metaphor; a 'useless and essentially superstitious notion' (Midgley 1994) and rejects it on the grounds that unless we can show “what kind of entity memes are purported to be, the parallel between them and genes surely vanishes, and the claim to scientific status with it.” (Midgley 2003 p 97). Gould points out many significant differences between genes and memes, and suggests that comparisons between biological and cultural evolution ‘have done more harm than good’ (Gould 1991). And McGrath claims that the “case for the existence of the ‘meme’ rests on the questionable assumption of a direct analogy with the gene, which proves incapable of bearing the theoretical weight that is placed upon it” (2005 p 121).

All these miss the point of Dawkins’ reason for inventing the term, which was not to draw an analogy but to illustrate the power of universal Darwinism by treating cultural information as another example of a replicator. Understanding this shows that analogies between genes and memes are secondary to the basic idea, not primary. Some analogies will be fruitful because memes and genes are both replicators, but others will not because memes use entirely different copying mechanisms from genes, totally different sources of variation, and different means of storing information. As Richerson & Boyd point out, “the best evidence suggests that cultural variants are only loosely analogous to genes” (2005 p. 60). This should not be a reason for rejecting memetics.

Another point to remember is that genes and their methods of replication have co-evolved for approximately four billion years, creating a high fidelity system with effective error-correction machinery, and often separating phenotypes from a germ line; whereas memes have been here for at most a few million years. In Dawkins’ terms, they are still in their ‘primeval soup’. We should therefore use gene-meme analogies cautiously, using them to build hypotheses, but not assuming precise similarity.

Another problem concerns the location or substance of memes. Are they to be thought of as residing in their physical substrate, whether that is human brains or the physical culture they create or both, or whether they should be considered as substrate-neutral informational entities. For example, if I tell you an excellent joke and you pass it on to someone else, and they pass it on again, we might want to ask whether this meme is the precise wording of the joke as told, the gist of the joke, the spoken words as sounds, or the representations of any of these inside people’s heads?

But this introduces unnecessary confusion. Memeticists themselves have mostly avoided this problem because they treat ‘that which is imitated’ as abstract information. This includes Dawkins

(1976) himself as well as Dennett (1995) and many others since. For example, Schlaile *et al* (2024) advocate taking an 'informational' rather than 'material' approach, and Boudry (2018) defends a purely abstract and information-theoretic definition of replication. In 'Parasites of the mind' he and Hofhuis (2018) favour a tolerance for fuzziness; 'If some piece of cultural information exhibits appreciable functional coherence, and is spreading through a population forming lineages of descent, then we can individuate that piece of information and give it a convenient name.' That name might be meme, culturgen, or more traditional terms such as ideas, habits, or beliefs.

Perhaps the greatest confusion has concerned the question of units. Memes are often described as "units of culture" or "units of imitation", although other descriptions include "elements of culture," "contagious ideas," or "cultural instructions". Some critics have made the problem of units into a major objection. For example, Midgley (2000) complains that culture cannot be neatly divided up into units, and nothing is to be gained by "atomising thought," since "thought is not granular" (p. 67). Similarly, Jablonka & Lamb (2014) argue that, in cultural evolution, there are no discrete unchanging units with unchanging boundaries that can be followed from one generation to the next, and Richerson & Boyd (2005) object to the idea that "culture must be divisible into tiny, independent gene-like bits that are faithfully replicated" or "tiny snippets of information" (p. 60). However, in defining memes as "discrete, faithfully replicating, gene-like bits of information," (p. 6) they are departing far from the original definition. Some memes are discrete and some are not; some replicate with very high fidelity (e.g., printed text or digital images) and some do not (e.g., gestures and physical actions); so memes may be like genes in some ways and not in others. Going back to the original idea of memes as information that is copied, or "that which is imitated," avoids these unrealistic claims.

This may be because the problem of units only arises because it is easier to talk about entities than to talk about "that which is imitated," in the abstract. Dennett tackles the problem head-on, calling memes 'mindless informational things' (2017 p 173) and 'a new kind of evolutionary replicator – culturally transmitted informational entities' (2017 p 175). He argues for defining the units as "the smallest elements that replicate themselves with reliability and fecundity" (1995 p. 344), or as a cultural item "with enough Design to be worth saving – or stealing or replicating." (p. 143). In art, for example, an entire gallery is too large a unit for selection to work on; but a blob of pink paint is too small. The single painting is the natural unit, as when we remember Picasso's *Guernica* or buy postcards of Monet's *Water Lilies*. A single word is too short to copyright and an entire library too long, but we can and do copyright three-word advertising jingles and 300,000-word books. A favourite musical meme is the first four notes of Beethoven's Fifth Symphony, a tiny unit

which has spread across the globe, probably even more widely than the larger unit represented by CDs and downloads of the whole work. In all these cases, both large and small amounts of information can count as a meme because they are copied as a unit with sufficient reliability and fecundity for selection to operate. In this view it is not a problem whether memes have to be considered as units or not.

Chvaja (2020) even claims that memetics has failed because memeticists are biased towards working on the ontology of meme units and predisposed to believe that evolution requires discrete units of selection. He suggests that this is because memetics originated in a gene-centered and anti-group-selectionist argument. Yet it has mostly been memetics' critics who have worried about units. Memeticists themselves, taking an abstract or information-theoretic approach, do not need to agonise over the units problem.

Vehicles, phemotypes, and the Lamarck objection

These often unproductive debates are complicated by the question whether memes have the equivalent of vehicles, interactors or phenotypes. By analogy with genes, these would be some kind of physical product of memetic information that acts as a vehicle or interactor for the meme itself, and are sometimes referred to as a 'phemotype' (Speel 1997), but this is another example where trying to draw close analogies with genes leads to confusion. Thinking about that joke, should we say that the meme itself is the joke and its phemotype is the information stored in the person's brain, or the written version, or what? Or thinking about a cake recipe, is the meme the cake itself, the written recipe, or the abstract instructions for making the cake? And if the latter, is the phemotype the cake, the written or spoken or videoed instructions, or what?

People have argued each way without reaching any consensus, and just to complicate the issue, Dawkins himself changed his mind. In *The Selfish Gene* (1976), he made no distinction between memes and their vehicles. Later, in *The Extended Phenotype* (1982) he revised this, making "the distinction between the meme itself, as replicator, on the one hand, and its 'phenotypic effects' or 'meme products' on the other. A meme should be regarded as a unit of information residing in a brain" (1982 p. 109). These two views are sometimes known as "Dawkins A" and "Dawkins B" (Gatherer, 1998).

Even before Dawkins coined the term 'meme', Cloak (1975) distinguished between i-culture (cultural instructions inside people's heads) and m-culture (the products of those instructions); the ultimate function of both being to maintain the i-culture. Subsequently others proposed that memes are neural patterns inside brains, with their products or vehicles being outside the brain (e.g. Delius 1989, Aunger 2002), or "an information pattern, held in an individual's memory, which is capable of

being copied to another individual's memory" (Heylighen and Chielens 2009). By contrast, Benzon (1996) argues precisely the opposite: that the replicators are outside brains and their vehicles inside.

This debate has been used by some to discredit or reject memetics (e.g. Jablonka & Lamb 2005, Wimsatt 1999) but others simply avoid it by reverting to the basic idea that memes are whatever is copied; so sounds, written text, physical objects and effects inside brains can all be considered as memes. This might make sense considering that memes are a relatively new replicator that has not settled down into an efficient system with vehicles or interactors distinct from the memes themselves (e.g. Blackmore 1999, Dennett 1995, Speel (1997).

This problem of distinguishing vehicles from replicators has given rise to further contentious and unresolved arguments that memetic inheritance is 'Lamarckian' (involving the inheritance of acquired characteristics) and that cultural variation is directed, not random (Aunger, 2000, Gould 1991, Richerson & Boyd, 2005). For some critics, these seem to rule out memetics as a valid enterprise, while others are more concerned with whether culture can evolve if these two claims are true (Kronfeldner, 2007). Yet the concern over Lamarckism is misplaced because the whole idea of calling memetic evolution "Lamarckian" rests on drawing a memotype/phenotype distinction which may be false (Blackmore 1999). For example, Sperber and Claidière claim there is nothing 'resembling a cultural germline' (2008 p 285). This is true for any memes that are naked replicators, having no phenotypes. This might include gossip passed from person to person by mouth, or funny facial expressions or actions that are imitated without ever being recorded. In these examples there are no intermediate steps or physical products so any suggestion of Lamarckism is irrelevant. For other examples it may not be.

As with previous disputes it may help to step back and remember the difference between one very old replicator (genes) and one very new replicator (memes). Genes are part of an ancient system that has been evolving for about four billion years, probably from simpler precursor systems (Maynard Smith and Szathmary 1995), creating an extraordinarily complex and high-fidelity system that produces all manner of creatures based on the recombination and mutation of information stored in a single type of molecule. The protection of information in the germ line and the separation of the genotype from phenotype was a critical step because it is more effective to copy the instructions for making something than it is to copy the product itself (Blackmore 1999, 2001). This is not only because multiple copies are made from the same instructions (increasing fecundity), but also because any accidents that befall the product – for example, during its construction or lifetime – are not passed on (increasing fidelity). An example is my hand. I was born with two fingers fused together and others abnormally short, but my children have normal-sized fingers and hands because I passed on genes, not the shape of the hand itself. This system not only avoids repeating accidents and

mistakes but more effectively retains any "good tricks" that the evolutionary exploration of design space stumbles upon (Dennett 1995).

By contrast, the first memes can have appeared only when our ancestors began to imitate with sufficient fidelity to sustain cumulative culture. Although we have no clear idea of what those early memes were, we can guess that they might include ways of lighting and maintaining fires, carrying and preparing food, or covering and decorating the body. When anyone acquired any such new skill they would have done so by observing someone else doing it first, fitting Thorndike's (1898) well-known definition of imitation as 'learning to do an act from seeing it done'. This was Dawkins' 'primeval soup' of culture.

A few million years later, many memes are still in this state, being naked memes with direct, low fidelity copying, no distinct generations, and a wide variety of copying methods. Others are not, and we may be seeing clear signs of culture evolving towards the much more efficient system of separated germ line and phemotype. For example, there is no phemotype when people hear someone sing or play an instrument and try to copy what they hear. This can be called copy-the-product. There is one if we like the music and download it from copies that are stored, with close to perfect fidelity, elsewhere. When you buy a film on DVD, it was not copied from a previous version of that film (i.e. copy-the-product); instead, multiple copies of the film were produced in a factory from the same original, making the equivalent of a germ line. This is copy-the-instructions for making the product and is a far better system for retaining information (Blackmore 2001). Damage to any particular copy does not matter because it does not affect subsequent copies. The same is true of printed books, cars, planes, and indeed anything made on a production line. Along with these changes, but only in the extremely brief period of the past century or so, has come the switch from analogue to digital storage which further improves fidelity. In these systems the argument about Lamarckism is meaningless.

Another argument against memetics that depends on making a questionable analogy with genes concerns the sources of variation. In biology, variation is mostly blind or random, produced by mutations and various processes of recombination. This is unlike the directed variation that occurs in so much of culture when we deliberately choose ways of altering memes or mixing memes together. Yet, the argument depends on assuming that blind variation is necessary for evolution to occur and this may not be so. Blind variation may be more effective than variation driven by human choices and expectations, but that does not mean that it is necessary. We might guess that cultural evolution will end up discovering and exploiting random variation. This is already happening with genetic algorithms used in evolutionary computation, and randomness plays important roles in much of the software we routinely use, and in the development of AI. All this suggests that memetic evolution is

discovering ever more effective means of implementing the evolutionary algorithm just as biology has been doing for billions of years.

A New Replicator or Culture on a Leash?

The whole concept of memes depends on the idea that memes are a new replicator, with their own replicator power, creating a new evolutionary process operating on top of the old. But is this valid?

One question concerns their methods of replication. The evolutionary algorithm requires that for behaviours to be truly replicated they must be *copied* with variation and selection. This implies an important difference between those that were already in the second individual's repertoire and were just evoked by what another person did or said, and those that were truly imitated, that is, they were new behaviours acquired by observing another individual (Thorndike 1898, Jablonka 1999). Sperber argues that a "fundamental objection to the meme model" is that most cultural items are "re-produced" in the sense of being produced many times, but are not "reproduced" in the sense of being copied from another (2000 p. 164). He compares two drawings, a more or less random scribble and a slightly wonky five-pointed star. When people try to copy them, the first is hard and results in a degenerating chain of copies; the second is easy and results in a series that tends towards the familiar star shape. As Dawkins points out, an independent observer might easily be able to put the first set of drawings into the order in which they were made, but not the second; it is "self-normalizing" (Dawkins 1999).

Sperber sees this as a serious objection to memetics because the drawing is not copied or imitated but is "re-produced", meaning it cannot count as a replicator, whereas Dawkins sees it as an example of the fidelity of meme transmission increasing as people learn to recognise and draw familiar shapes. This same increase in fidelity happens when people learn to speak, dividing the space of possible sounds into a limited number of discrete words that can then be mixed in potentially infinite ways. Reading and writing further increase fidelity, as well as the longevity and fecundity of written memes. Similar, although perhaps less obvious, developments can be seen in chess moves, dance steps, sports, cooking and many other everyday learned skills.

It may be useful to think in terms of a spectrum with evocation at one end and true transmission at the other (Morin, 2015). Many examples would be somewhere in between. This might include the drawing of the five-pointed star. Indeed passing on gossip, news, and stories, or writing books and emails, involves the evocation of words already known by the listener. What is new is the order they are put in.

Boudry (2018) analyses the notion of 'replication' applying an abstract information-theoretic approach that applies equally to genes and memes. He proposes a distinction between 'evocation'

and ‘extraction’ of cultural information. In evocation, the message (whether that’s a drawing, a story, or any other kind of cultural information) is already in the receiver’s repertoire and is merely being triggered by a stimulus. So in this case no true replication is occurring. By contrast, in extraction, the previous knowledge the receiver has is still used but this is in order to recreate or decode what is being passed on. In this case the message is new and surprising to the receiver even though prior knowledge is involved. It does not matter that the process of extraction can be complex or circuitous; if the message received is new and surprising, replication has taken place.

Can we then conclude that memes are replicators? Richerson and Boyd reject memetics by claiming that “cultural variants are not replicators” (2005, p. 82), citing the peculiarities of biased transmission, behavioural attractors, and error prone imitation. However, this may show only how complex memetic transmission or extraction can and must be (Blackmore 2010; Boudry, 2018). They also contend that copying must be perfect for a replicator to count as such, suggesting that memes must be “discrete, faithfully replicating, genelike bits of information” (2005 p 6) but to expect memes to be just like genes is another unhelpful analogy. What matters for genes, as for memes, is not the precise method of storage and replication but the information that is replicated. Also, if copying were perfect, whether of genes or memes, there would be no variation on which selection could operate and therefore no evolution. Human imitation is far from perfect and, as we have seen, transmission of ideas, habits, and stories, involves all sorts of extraction methods. Yet it is clearly good enough to sustain a rich and expanding cumulative evolutionary process.

Among theories of cultural evolution, the major alternative to memetics is dual-inheritance theory or gene-culture co-evolution (for explanation and critiques see Richerson & Boyd, 2005; Richerson, 2017). These tend to follow Lumsden and Wilson’s famous claim that “genetic natural selection operates in such a way as to keep culture on a leash” (1981, p 13). In other words, culture is an adaptation of benefit to human genes and, ultimately, kept under control by them. This makes an important difference. For memetics, memes did not evolve primarily as an adaptation of benefit to genes; they were a new replicator that was accidentally let loose by the human capacity for imitation and they may be either adaptive or maladaptive from the genes’ point of view.

The earliest memes would probably not have survived had they not been biologically adaptive, and even now many memes are still adaptive such as religious memes that instruct followers to have many children and to bring them up in the faith. But as culture evolved ever faster, fewer and fewer memes have been directly adaptive for human genes. Indeed some, such as effective methods of birth control, act directly against the interests of human genes. Religions are full of biologically useful memes but in many parts of the world are giving way to the concept of human rights, of freedom of the individual, equality, and women’s rights, and birth rates are falling fast.

In 1976, when he first coined the term ‘meme’, Dawkins complained of his colleagues that “In the last analysis they wish always to go back to ‘biological advantage’” (p. 193). Richerson and Boyd provide a perfect example. Their ‘costly information hypothesis’ comes very close to memetics in some ways; they occasionally use the term “selfish meme” and describe us, and our culture, as like obligate mutualists. Yet they still maintain that “culture is an adaptation” and that “culture is on a leash, all right” even if the dog on the end is clever and strong.

This is especially clear when it comes to the highly contentious issue of the origins of language. Most theories assume that language must have evolved as an adaptation, i.e. using language was adaptive for early humans’ genes. Although this may seem obvious, memetics does not assume this but instead sees language, like the rest of culture, as a parasitic second-level replicator that appeared when our ancestors became capable of imitating sounds and extracting information from other people. These new, imitated behaviours required energy, time and brain power both to acquire and retain. In this view, our relatively enormous brains were a burden created by memetic drive, by the demand to become ever better at imitation when the meme pool expanded. And human language was not originally a biological adaptation but a parasite turned symbiont (Blackmore 1999, 2007).

Both memetics and gene-culture co-evolution theories claim that brains and language have shaped each other (Blackmore 2008, Christiansen and Chater 2008) but again with the same fundamental difference. Most theories appeal to genetic advantage to explain this process and either reject or ignore memetics altogether (e.g. Botha and Everaert 2013, Christiansen et al 2009, Chater and Christiansen 2010). As though this nullifies the value of any memetic analysis, some point to sources of variation, claiming that memes ‘seem patently to be products of sighted watchmakers; that is, they are products, in part at least, of many generations of intelligent designers, imitators, and critics.’ (Christiansen et al 2016 p 61). This is not a valid way of rejecting memetics though, because of the way that replication or extraction inevitably involves complex processes dependent on prior knowledge. For example, for you to understand anything in this book, you must have acquired language, learned to read, and had long years of education, but you would not be reading it at all if it did not provide new or surprising ideas that you did not already have.

Animal culture

There are two important questions to ask when thinking about animal culture in the light of memetics. First, do animals other than humans have culture? Second do they have memes? The answer to the first is yes: the answer to the second is less certain.

Twenty years ago there would have been great scepticism with respect to applying the term 'culture' to species other than humans. Although regional dialects in bird song and cetaceans, and behavioural differences between groups of chimpanzees were known about, the idea that these constituted culture was still in question. That has changed with ever increasing evidence of behavioural traditions and cultural differences between groups in many other species. (Whiten, 2021). These include birds, fish, and even invertebrates, and the behaviours range from foraging techniques and tool use to vocal communication, migratory pathways, courtship displays, and nesting sites.

In the late twentieth century research on chimpanzees revealed multiple differences between distinct groups in grooming behaviour, foraging techniques, and tool use – most famously using tools to fish for termites or crack open nuts. An ethnographic study found ten wild communities of chimpanzees that use sticks to fish in termite mounds and nests, and showed that they use distinctly different combinations of actions to do so (Boesch, 2020). Among groups in West Africa, some have traditions of cracking open certain kinds of nuts while others, living not far away, crack different nuts or none at all. That this behaviour is cultural rather than innate has been shown in experiments in which captive chimpanzees were unable to invent nut cracking on their own and succeeded only when the skill was first demonstrated. Then in field experiments in West Africa, researchers provided nuts, stones, palm fruit, and cracked palm nuts in a natural setting. Groups of chimpanzees visited the site but after three study periods totalling a year, none had spontaneously begun cracking nuts with the stones provided (Koops *et al*, 2022).

In primates there seem to be three main phases of social learning, first between an infant and its mother, then through juvenile networks, and finally when adults disperse to different groups (Whiten & van de Waal, 2018). Individuals have been observed following the most successful nut-crackers or foragers which might enhance the accurate spread of new behaviours. This is just one social learning strategy for deciding what and whom to copy (Kendal *et al*, 2018). Other transmission biases include conforming to the majority, copying the highest status individual, and those based on the observers' state, or the content of what is learned.

Social learning has been demonstrated in whales and other cetaceans. For example, a 'cultural revolution' has been described when a new humpback whale song is recorded and then found to spread rapidly across populations (Whitehead & Rendell, 2014). Juveniles follow mothers on annual migrations between their breeding and feeding grounds to learn the traditional routes to follow. There are complex and stable vocal and behavioural cultures in clans of killer whales, for example, displaying quite different hunting traditions, such as specializing in seal versus fish as prey.

These, and many other studies have revealed a rich variety of cultural traditions, with good evidence that their spread and maintenance requires social, not only individual, learning. There are suggestions of gene-culture co-evolution in which long-lasting cultural differences may eventually lead to speciation (Whiten, 2021). Culture has typically been considered to be species-specific but the concept of co-culture or co-cultural evolution applies when two populations of different species influence each other's learned behaviours through mutual cultural evolution, resulting from shared adaptations within the same environment. One example involving humans is honeyguides in Tanzania and Mozambique, where these birds lead humans to honeybee nests and the birds and human both benefit. Another is when wild birds adapt to human urban environments and people provide food for them. Examples of co-culture between other species include cooperative scavenging between ravens and wolves, cooperative hunting between false killer whales and bottlenose dolphins, and the sharing of signals between distinct species of tamarin. Potentially this process, too, could drive gene-culture co-evolution (Sueur & Huffman, 2024).

But there remain many questions about the skills used in the transmission of animal cultures and whether they can be considered to involve a new replicator and cumulative culture as would be the case for memetic evolution. For a new replicator to be involved animals must be capable not only of reproducing old behaviours by observing others performing them but creating new ones and varying old ones that can be passed on and subject to selection. The question then is whether other forms of social or individual learning can do this.

Contagion is a clear example of non-memetic transmission. For example, coughing, yawning and laughing can all be contagious, spreading quickly through groups of people. But laughing when someone else laughs, or joining in a spate of annoying coughing at a concert, involves no copying. The second person’s laugh is triggered by hearing the first, and is their own laugh, not a copy of the first person’s laugh (that is, unless they are deliberately mimicking). Contagion in other species includes picking up a warning cry from another, or fleeing when another does. This is entirely triggered re-production or evocation, and is neither cultural nor memetic.

Two famous examples illustrate the way animal culture can arise through social learning processes other than imitation; tits opening milk bottles in England and macaques washing sweet potatoes in Japan.

Throughout much of the twentieth century in England, unhomogenised milk (in which the cream rises to the top) was delivered to people’s doors in glass bottles with shiny silver or gold-coloured foil tops, and in 1921 a new phenomenon was observed; the foil tops were found broken and jagged. The culprits turned out to be various small birds, mostly blue tits (*Cyanistes caeruleus*), and the new behaviour spread from village to village, having started at several separate locations

(Fisher and Hinde 1949). This can be thought of as bird culture but was this spreading innovation a meme; would it count as a replicator? In other words, did it spread by a process capable of sustaining copying with variation and selection? The answer may be no; although this looks like imitation, the new behaviour might have spread by stimulus enhancement rather than imitation (Sherry & Galef 1984). Blue tits often tear at bark or leaves to find food, and peck to eat it, and experimental studies have shown that blue tits, especially juvenile females, are proficient at social learning and this ability is correlated with innovative problem solving (Aplin et al 2013). It is therefore not surprising that some birds may have tried the foil tops and discovered the rich cream underneath. They would then have left jagged silver tops which would be conspicuous to other birds who might then also discover the cream and associate this treat with milk bottles (Sherry & Galef 1984). On this account, the birds had not learned a new skill from seeing it done, but only a new stimulus at which to tear and peck. Another possibility is that they learned through local enhancement, learning they could find cream near houses' front doors. There was no indication of variations in the behaviour that could be selected, and no evidence of cumulative culture suggesting a true replicator.

Similar doubt can be cast over the case of the Japanese macaques on Koshima Island who, in 1948, were found to be taking the sweet potatoes that were provided for them, and washing the sand off them in the sea (Hirata et al 2008). This new cultural behaviour was long thought to have been spread by imitation but there are other possibilities. Macaques seem to enjoy water and there are many other instances of groups that regularly go into rivers or pools. Juveniles also tend to follow their mothers. So it is possible that some individuals accidentally discovered that sweet potatoes dropped into the sea were nicer to eat. Then, by following them, others discovered the trick for themselves. This would enable an animal culture but not one that could evolve by generating variations available for selection. In other words, sweet potato washing is not a meme. We can then ask the second question, do any other animals have memes?

If a meme is defined as that which is imitated, as Dawkins originally defined it, then we should conclude that other species have memetic culture only if they can imitate, and imitate well enough to give rise to copying with variation and selection. However, the situation is not that simple because not everyone agrees with defining memes this way and even Dawkins referred to 'imitation in the broad sense' which might allow other types of social learning to count as creating memes. Also, human cultural transmission involves a lot more than imitation, including the ability to create and copy variations of memes, to extract meaning from others using prior learned information and language, and to remember vast amounts of the information gained.

Even so, it is useful to ask whether other species are capable of true imitation, and there is a long history of speculation on the topic (Bonner, 1980; Galef, 2013; Nehaniv et al, 2002, Thorndike,

1898). Song birds imitate sounds, and there have been several studies of bird song memes and their survival and propagation in the meme pool. The brain changes entailed in such imitative learning have been studied in zebra finches that listen to their father's song from about a month after hatching and practise each song hundreds of thousands of times (Vallentin et al 2016), and the evolutionary origins of vocal imitation in songbirds has been tracked and found to have evolved repeatedly within the songbird clade (Goller & Shizuka, 2018).

Many cetaceans and some apes are known to be capable of imitation and have been studied both in the wild and the laboratory (Whiten (2001). Recent experimental studies have used methods such as the 'do-as-other-does' paradigm in which animals learn to copy familiar and novel behaviours by watching a demonstrator. Killer whales, for example, have been shown to acquire novel behaviours this way (Abramson et al 2013). Dolphins have been taught to imitate on demand, can imitate both other dolphins and humans, and are capable of deferred imitation, with juveniles more often displaying spontaneous imitation, and adults being better at elicited imitation (Kuczaj & Yeater 2006).

Such studies show that some species are capable of true imitation. But do the copied behaviours then necessarily count as memes? And can they sustain evolving cultures? Fierce arguments have concerned the comparison between human imitation and that of the other great apes, with disputes over the question of whether 'apes ape' (Tomasello 1993, Whiten *et al*, 2004). Some have argued that while children are true imitators, chimpanzees display only emulation. In other words they copy only the goal of an observed behaviour, such as gaining food, and use their own methods for completing the task (see Whiten et al 2009 for a review).

Experimental studies comparing children with chimpanzees have provided intriguing results suggesting 'overimitation' in children but not in other apes. That is, children readily imitate specific actions even when these do not obviously lead to any reward, are irrelevant to the demonstrated outcome, and even when there are more efficient methods of achieving the demonstrated outcome or their own actions result in failure (Nielsen, 2009). Overimitation has been defined as the 'imitation of perceivably causally unnecessary actions in relation to the goal of an action sequence performed by a model' (Hoehl *et al*, 2019).

To explore this, in some experiments demonstrators used a mixture of relevant and irrelevant actions to open an 'artificial fruit' with food or a toy inside; when the box containing a reward was opaque both children and chimpanzees copied the demonstrated actions fairly accurately but when it was transparent and they could see that some actions were irrelevant to opening the box, the children continued to copy all the actions while the chimpanzees used only relevant actions. In another study, two-year-old children, chimpanzees, and orangutans were shown how to open a plastic tube to get at

food or a toy inside. Whereas the children mostly copied the demonstrated actions the other apes tended to try to smash or tear their way into the tube (Horner & Whiten, 2005, Nielsen 2009, Whiten 2017). Similar differences were observed comparing 3 to 5 year-old children with bonobos; the children readily copied causally irrelevant actions whereas none of 46 bonobos did so (Clay & Tennie 2017).

Why would children do this seemingly pointless activity potentially wasting time and energy? Indeed why would adults do this too, carrying out actions that are clearly not causally related to a desired goal? A particularly striking example of an apparently pointless imitation is the Melanesian culture of 'cargo cults' in which, following the arrival of colonial invaders in ships and planes, people built rough imitations of planes and radio stations, hoping to invoke their ancestors to bring cargo (Hoehl *et al*, 2019). Today, the spread of clothes fashions, music choices, Internet memes, conspiracy theories, and much else in modern culture, depends on imitating things that are far from biologically adaptive.

This difference between us and other species could be highly significant from a meme's eye point of view. Overimitation means copying almost any demonstrated memes; emulation (or goal emulation) means that only memes perceived by the animal as useful or relevant to its goals are copied and this makes a difference. Overimitation is hard to explain from a biologically adaptive point of view, although possibly it could serve affiliation with the model (Keupp, Behne, & Rakoczy; 2013). But it is easy to explain from a meme's eye perspective. If memes are replicators, the tendency to copy all or any actions is a far more effective basis for their evolution because it provides more actions, more variation in actions, and therefore greater scope for selection to operate. Overimitation is precisely what would be needed to let loose a second replicator which would then evolve in its own direction for its own benefit, competing with genetic evolution. This is where the difference lies between gene-culture co-evolution theory and memetics. It comes back to the '*Cui bono*?' question. In gene-culture co-evolution theory, the beneficiary of behavioural abilities is ultimately genes. For memetics it is the memes themselves that benefit.

Looked at this way, human cumulative culture really is different from the cultures of other species. The strongest form of this argument would be to say that it is the capacity for true imitation, and especially overimitation, that distinguishes human culture from other animals' culture because only this gives rise to the variation and selection of new variants that is necessary for a new evolutionary process to take off.

If imitation is so powerful, it might seem surprising that it has not evolved more widely. But this is not necessarily so, not only because indiscriminate copying is rarely beneficial (Kendal *et al* 2018) but because a second replicator can exploit its hosts with unpredictable consequences. Also,

imitation requires considerable cognitive ability and storage space, which has driven the expansion of the human brain (Blackmore 2001, Richerson & Boyd, 2005). This may be why we humans are the only species known to have developed the potential for memetic evolution and cumulative culture.

Memetics' future

For decades after it was proposed in 1976, the concept of memes was widely ignored or derided and very little theoretical or experimental progress was made. Many reasons were suggested, including the need for discrete units of selection, the difficulty of making testable predictions, and people's fears that memetics would take away much of human self-determination and power. Little empirical work and few applications of memetics were made, but that has changed.

The advent of Internet memes created a new world for meme research, starting at the end of the last century with studies of how memes spread (Pocklington & Best, 1997; Miltner, 2018). There are studies of the use of humour, and the evolution and globalisation of jokes (Shifman & Thelwall 2009, Shifman et al 2014; Wagner & Schwarzenegger, 2020), the impact of memes on society and values (Denisova, 2019; Shifman, 2019) and the ways that Internet memes can be used to promote critical thinking and learning (Wells, 2018; Reddy et al, 2020). Other topics include the evolution of music and musical notation (Jan 2017), a comparison of the evolution of chemical terms in Chinese and Western science (Wright 2000), their impact on art and design (Steadman 2008). Memes have been analysed as meaning-making (Wiggins, 2019) and considered as signs in semiotics or as standing for the rules of how a cultural practice is performed (Cannizzaro, 2016; Fomin, 2019). Memetics has been widely applied in evolutionary economics (Schlaile, 2021; Schlaile, Veit & Boudry, 2024). All this suggests that the idea of a second replicator structuring human society, beliefs, and behaviour is gaining traction and proving useful.

The appearance of a second replicator may not be the end for evolution on Earth. I have suggested a further possibility based on universal Darwinism, that perhaps further replicators might piggy-back on existing ones. Memes arose when one of the products of genes became capable of a new kind of copying – imitating sounds and actions. I have suggested that a third replicator might, in an analogous process, emerge from products of the second. Such new replicators may already be emerging as digital information copied by computers, phones, servers and other devices (Blackmore 2010). I initially referred to these new replicators as 'temes' but when this caused much confusion I changed the name to 'treme'. Tremes are digital information copied, varied and selected by silicon based technology, independent of human control. That they are increasingly independent of our

control is illustrated by the burgeoning of artificial intelligence and systems that communication with each other without human intervention. If this is correct then tremes would provide another example of a selfish replicator, blindly propagating for its own benefit rather than for the benefit of human beings, their genes, their technology, the other animals with which we share our world, or the environment in which we all live. This is not a process that we can now take back or stop. We would do well to understand it as best we can.

Conclusion/Summary

Memetics is based on the principle of universal Darwinism, that when information is copied, varied and selected, evolution must occur whether that information is encoded in chemistry as for genes, or in cultural activities as memes are. For memetics, memes are selfish information in the same way that genes are, spreading for its own benefit, not necessarily for that of us humans, our societies, or our genes. Other theories of cultural evolution, especially gene-culture co-evolution theory, do not accept that memes are replicators. Criticisms of memetics are explored but many are falsely based on expecting a close analogy with genes when the mechanisms of replication are entirely different. The advent of Internet memes and now the rapid growth of social media and artificial intelligence, suggest the possibility that a third replicator, based on the digital technology we have provided, is already evolving, with unknown consequences for us and the planet.

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