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EVOLUTION AND MEMES: THE HUMAN BRAIN AS A SELECTIVE IMITATION DEVICE

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The meme is an evolutionary replicator, defined as information copied from person-to-person by imitation. I suggest that taking memes into account may provide a better understanding of human evolution in the following way. Memes appeared in human evolution when our ancestors became capable of imitation. From this time on, two replicators—memes and genes—coevolved. Successful memes changed the selective environment, favoring genes for the ability to copy them. I have called this process memetic drive. Meme-gene coevolution produced a big brain that is especially good at copying certain kinds of memes. This is an example of the more general process in which a replicator and its replication machinery evolve together. The human brain has been designed not just for the benefit of human genes, but for the replication of memes. It is a selective imitation device. Some problems of definition are discussed and suggestions made for future research.

The concept of the meme was first proposed by Dawkins (1976) and since that time has been used in discussions of (among other things) evolutionary theory, human consciousness, religions, myths, and mind viruses (e.g., Dennett, 1991, 1995; Dawkins, 1993; Brodie, 1996; Lynch, 1996). I believe, however, that the theory of memes has a more fundamental role to play in our understanding of human nature. I suggest that it can give us a new understanding of how and why the human brain evolved, and why humans differ in important ways from all other species. In outline, my hypothesis is as follows.

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Everything changed in human evolution when imitation first appeared because imitation let loose a new replicator—the meme. Since that time, two replicators have been driving human evolution, not one. This is why humans have such big brains, and why they alone produce and understand grammatical language, sing, dance, wear clothes, and have complex cumulative cultures. Unlike other brains, human brains had to solve the problem of choosing which memes to imitate. In other words, they have been designed for selective imitation.

This is a strong claim and the purpose of this paper is first to explain and defend it, second to explore the implications of evolution operating on two replicators, and third to suggest how some of the proposals might be tested. One implication is that we have underestimated the importance of imitation.

THE NEW REPLICATOR

The essence of all evolutionary processes is that they involve some kind of information which is copied with variation and selection. As Darwin (1859) first pointed out, if you have creatures that vary, and if there is selection so that only some of those creatures survive, and if the survivors pass on to their offspring whatever it was that helped them survive, then those offspring must, on average, be better adapted to the environment in which that selection took place than their parents were. It is the inevitability of this process that makes it such a powerful explanatory tool. If you have the three requisites—variation, selection, and heredity—then you *must* get evolution. This is why Dennett calls the process the evolutionary algorithm. It is a mindless procedure which produces ‘‘design out of chaos without the aid of mind’’ (Dennett, 1995, p. 50).

This algorithm depends on something being copied, and Dawkins calls this the replicator. A replicator can, therefore, be defined as any unit of information that is copied with variations or errors, and whose nature influences its own probability of replication (Dawkins, 1976). Alternatively, one can think of it as information that undergoes the evolutionary algorithm (Dennett, 1995) or that is subject to blind variation with selective retention (Campbell, 1960), or as an entity that passes on its structure largely intact in successive replications (Hull, 1988).

The most familiar replicator is the gene. In biological systems genes are packaged in complex ways inside larger structures, such as organisms. Dawkins, therefore, contrasted the genes as replicators with the vehicles that carry them around and influence their survival. Hull prefers the term interactors for those entities that interact as cohesive wholes with their environments and cause replication to be differential (Hull, 1988). In either case, selection may take place at the level of the organism (and arguably at other levels), but the replicator is the information that is copied reasonably intact through successive replications and is the ultimate beneficiary of the evolutionary process.

Note that the concept of a replicator is not restricted to biology. Whenever there is an evolutionary process (as defined above), then there is a replicator. This is the basic principle of what has come to be known as universal Darwinism (Dawkins, 1976; Plotkin, 1993) in which Darwinian principles are applied to all evolving systems. Other candidates for evolving systems with their own replicators include the immune system, neural development, and trial-and-error learning (e.g., Calvin, 1996; Edelman, 1989; Plotkin, 1993; Skinner, 1953).

The new replicator I refer to here is the meme—a term coined in 1976 by Dawkins. His intention was to illustrate the principles of universal Darwinism by providing a new example of a replicator other than the gene. He argued that whenever people copy skills, habits, or behaviors from one person to another by imitation, a new replicator is at work.

> ‘‘We need a name for the new replicator, a noun that conveys the idea of a unit of cultural transmission, or a unit of *imitation*. ‘Mimeme’ comes from a suitable Greek root, but I want a monosyllable that sounds a bit like ‘gene.’ I hope my classicist friends will forgive me if I abbreviate mimeme to *meme* ... Examples of memes are tunes, ideas, catch-phrases, clothes fashions, ways of making pots, or of building arches. Just as genes propagate themselves in the gene pool by leaping from body to body via sperms or eggs, so memes propagate themselves in the meme pool by leaping from brain to brain via a process which, in the broad sense, can be called imitation.’’ (Dawkins, 1976, p. 192).

Dawkins now explains that he had modest, and entirely negative, intentions for his new term. He wanted to prevent his readers from thinking that the gene was necessarily the ‘‘be-all and end-all of evolution ... which all adaptations could be said to benefit" (Dawkins, 1999, p. xvi) and make it clear that the fundamental unit of natural selection is the replicator—*any* kind of replicator. Nevertheless, he laid the groundwork for memetics. He likened some memes to parasites infecting a host, especially religions which he termed "viruses of the mind" (Dawkins, 1993), and he showed how mutually assisting memes will group together into coadapted meme complexes (or memeplexes) often propagating themselves at the expense of their hosts.

Dennett subsequently used the concept of memes to illustrate the evolutionary algorithm and to discuss personhood and consciousness in terms of memes. He stressed the importance of asking *Cui bono*? Or who benefits? The ultimate beneficiary of an evolutionary process, he stressed, is whatever it is that is copied, i.e., the replicator. Everything else that happens, and all the adaptations that come about, are ultimately *for the sake of* the replicators.

This idea is central to what has come to be known as selfish gene theory, but it is important to carry across this insight into dealing with any new replicator. If memes are truly replicators in their own right, then we should expect things to happen in human evolution that are not for the benefit of the genes, nor for the benefit of the people who carry those genes, but for the benefit of the memes which those people have copied. This point is absolutely central to understanding memetics. It is this which divides memetics from closely related theories in sociobiology (Wilson, 1975) and evolutionary psychology (e.g., Barkow, Cosmides, & Tooby, 1992; Pinker, 1997). Dawkins complained of his colleagues that "in the last analysis they wish always to go back to 'biological advantage'" (Dawkins, 1976, p. 193). This is true of theories in evolutionary psychology but also of most of the major theories of gene-culture coevolution. For example, Wilson famously claimed that "the genes hold culture on a leash" (Lumsden & Wilson, 1981). More recently, he has conceded that the term meme has won against its various competitors but he still argues that memes (such as myths and social contracts) evolved over the millennia because they conferred a survival advantage on the genes, not simply because of advantages to themselves (Wilson, 1998). Other theories such as the mathematical models of Cavalli–Sforza and Feldman (1981) and Lumsden and Wilson (1981) take inclusive fitness (advantage to genes) as the final arbiter, as does Durham (1991), who argues that organic and cultural selection work on the same criterion and are complementary. Among the few exceptions are Boyd and Richerson's dual inheritance model (1985), which includes the concept of cultural fitness, and Deacon's (1997) coevolutionary theory in which language is likened to a parasitic organism with adaptations that evolved for its own replication, not for that of its host.

With these exceptions, the genes remain the bottom line in most such theories, even though maladaptive traits (that is, maladaptive to the genes) can arise, and may even thrive under some circumstances (Durham, 1991; Feldman and Laland, 1996). By contrast, if you accept that memes are a true replicator, then you must consider the fitness consequences for memes themselves. This could make a big difference, and this is why I say that everything changed in evolution when memes appeared.

When was that? If we define memes as information copied by imitation, then this change happened when imitation appeared. I shall argue that we should do just that, but this will require some justification.

PROBLEMS OF DEFINITION

If we had a universally agreed definition of imitation, we could define memes as that which is imitated (as Dawkins originally did). In that case, we could say that by definition, memes are transmitted whenever imitation occurs and, in terms of evolution, one could say that memes appeared whenever imitation did. Unfortunately, there is no such agreement either over the definition of memes or of imitation. Indeed, there are serious arguments over both definitions. I suggest that one may find a way out of these problems of definition by thinking about imitation in terms of evolutionary processes, and by linking the definitions of memes and imitation together.

In outline, my argument is as follows. The whole point of the concept of memes is that the meme is a replicator. Therefore, the process by which it is copied must be one that supports the evolutionary algorithm of variation, selection, and heredity—in other words, producing copies of itself that persist through successive replications, which vary and undergo selection. If imitation is such a process, and if other kinds of learning and social learning are not, then we can usefully tie the two definitions together. We can define imitation as a process of copying that supports an evolutionary process, and define memes as the replicator which is transmitted when this copying occurs.

Note that this is not a circular definition. It depends crucially on an empirical question—is imitation in fact the kind of process that can support a new evolutionary system? If it is, then there must be a replicator involved and we can call the replicator the meme. If not, then this proposal does not make sense. This is, therefore, the major empirical issue involved, and I shall return to it when I have considered some of the problems with our current definitions.

Defining the Meme

The *Oxford English Dictionary* defines memes as follows "**meme** (mi : m), *n*. Biol. (shortened from *mimeme* ... that which is imitated, after GENE *n*.) An element of a culture that may be considered to be passed on by non-genetic means, esp. imitation." This is clearly built on Dawkins's original conception, and is clear as far as it goes. However, there are many other definitions of the meme, both formal and informal, and much argument about which is best. These definitions differ mainly on two key questions: (1) whether memes exist only inside brains or outside of them as well, and (2) the methods by which memes may be transmitted.

The way we define memes is critical, not only for the future development of memetics as a science, but for our understanding of evolutionary processes in both natural and artificial systems. Therefore, we need to get the definitions right. What counts as right, in my view, is a definition that fits the concept of the meme as a replicator taking part in a new evolutionary process. Any definition that strays from this concept loses the whole purpose and power of the idea of the meme—indeed its whole reason for being. It is against this standard that I judge the various competing definitions, and my conclusion is that memes are both inside and outside of brains, and they are passed on by imitation. The rest of this section expands on that argument and can be skipped for the purposes of understanding the wider picture.

First, there is the question of whether memes should be restricted to information stored inside people's heads (such as ideas, neural patterns, memories, or knowledge) or should include information available in behaviors or artifacts (such as speech, gestures, inventions and art, or information in books and computers).

In 1975, Cloak distinguished between the cultural instructions in people's heads (which he called *i-culture*) and the behavior, technology, or social organization they produce (which he called *m-culture*). Dawkins (1976) initially ignored this distinction, using the term "meme" to apply to behaviors and physical structures in a brain, as well as to memetic information stored in other ways (as in his examples of tunes, ideas, and fashions). This is sometimes referred to as Dawkins A (Gatherer, 1998). Later (Dawkins B), he decided that "A meme should be regarded as a unit of information residing in a brain (Cloak's i-culture)" (Dawkins, 1982, p. 109). This implies that the information in the clothes or the tunes does not count as a meme. But later still he says that memes "can propagate themselves from brain to brain, from brain to book, from book to brain, from brain to computer, from computer to computer" (Dawkins, 1986, p. 158). Presumably, they still count as memes in all these forms of storage—not just when they are in a brain. So this is back to Dawkins A.

Dennett (1991, 1995) treats memes as information undergoing the evolutionary algorithm, whether they are in a brain, a book, or some other physical object. He points out that copying any behavior must entail neural change and that the structure of a meme is likely to be different in any two brains, but he does not confine memes to these neural structures. Durham (1991) also treats memes as information, again regardless of how they are stored. Wilkins defines a meme as "the least unit of sociocultural information relative to a selection process that has favorable or unfavorable selection bias that exceeds its endogenous tendency to change" (Wilkins, 1998). This is based on Williams's now classic definition of the gene as "any hereditary information for which there is a favorable or unfavorable selection bias equal to several or many times its rate of endogenous change" (Williams, 1966, p. 25). What is important here is that the memetic information survives intact long enough to be subject to selection pressures. It does not matter where and how the information resides.

In contrast, Delius (1989) describes memes as "constellations of activated and nonactivated synapses within neural memory networks" (p. 45) or "arrays of modified synapses" (p. 54). Lynch (1991) defines them as memory abstractions or memory items, Grant (1990) as information patterns infecting human minds, and Plotkin as ideas or representations "... the internal end of the knowledge relationship" (Plotkin, 1993, p. 215), while Wilson defines the natural elements of culture as "the hierarchically arranged components of semantic memory, encoded by discrete neural circuits awaiting identification" (Wilson, 1998, p. 148).

Closer to evolutionary principles, Brodie defines a meme as "a unit of information in a mind whose existence influences events such that more copies of itself get created in other minds" (Brodie, 1996, p. 32), but this restricts memes to being in minds. Presumably, on all these latter definitions, memes cannot exist in books or buildings, so the books and buildings must be given a different role. This has been done by using further distinctions, usually based on a more or less explicit analogy with genes.

Cloak (1975) explicitly likened his i-culture to the genotype and m-culture to the phenotype. Dennett (1995) also talks about memes and their phenotypic effects, though in a different way. The meme is internal (though not confined to brains), while "the way it affects things in its environment" (p. 349) is its phenotype. In an almost complete reversal, Benzon (1996) likens pots, knives, and written words (Cloak's m-culture) to the gene; and ideas, desires, and emotions (i-culture) to the phenotype. Gabora (1997) likens the genotype to the mental representation of a meme and the phenotype to its implementation. Delius (1989), having defined memes as being in the brain, refers to behavior as the memes' phenotypic expression, while remaining ambiguous about the role of the clothes fashions he discusses. Grant (1990) defines the "memotype" as the actual information content of a meme, and distinguishes this from its "sociotype" or social expression. He explicitly bases his memotype/sociotype distinction on the phenotype/genotype distinction. All these distinctions are slightly different and it is not at all clear which, if any, is better.

The problem is this. If memes worked like genes, then we should expect to find close analogies between the two evolutionary systems. But, although both are replicators, they work quite differently and for this reason we should be very cautious of meme-gene analogies. I suggest that there is no clean equivalent of the genotype/phenotype distinction in memetics because memes are a relatively new replicator and have not yet created for themselves this highly efficient kind of system. Instead, there is a messy system in which information is copied all over the place by many different means.

I previously gave the example of someone inventing a new recipe for pumpkin soup and passing it on to various relatives and friends (Blackmore, 1999). The recipe can be passed on by demonstration, writing the recipe on a piece of paper, explaining over the phone, sending a fax or e-mail, or (with difficulty) by tasting the soup and working out how it might have been cooked. It is easy to think up examples of this kind that make a mockery of drawing analogies with genotypes and phenotypes because there are so many different copying methods. Most important for the present argument, we must ask ourselves this question: Does information about the new soup only count as a meme when it is inside someone's head or also when it is on a piece of paper, in the behavior of cooking or passing down the phone lines? If we answer that memes are only in the head, then we must give some other role to these many other forms and, as has been seen, this leads to confusion.

My conclusion is this. The whole point of memes is to see them as information being copied in an evolutionary process (i.e., with variation and selection). Given the complexities of human life, information can be copied in myriad ways. We do a disservice to the basic concept of the meme if we try to restrict it to information residing only inside people's heads—as well as landing ourselves in all sorts of further confusions. For this reason I agree with Dennett, Wilkins, Durham, and Dawkins A, who do not restrict memes to being inside brains. The information in this article counts as memes when it is inside my head or yours, when it is in my computer, or on the journal pages, or when it is speeding across the world in wires or bouncing off satellites, because in any of these forms it is potentially available for copying and can, therefore, take part in an evolutionary process.

We may now turn to the other vexed definitional question—the method by which memes are replicated. The dictionary definition gives a central place to imitation, both in explaining the derivation of the word "meme" and as the main way in which memes are propagated. This clearly follows Dawkins's original definition, but Dawkins was canny in saying imitation "in the broad sense." Presumably he meant to include many processes that one may not think of as imitation but that depend on it, like direct teaching, verbal instruction, learning by reading, and so on. All these require an ability to imitate. At least, learning language requires the ability to imitate sounds, and instructed learning and collaborative learning emerge later in human development than does imitation and arguably build on it (Tomasello, Kruger, & Ratner, 1993). One may be reluctant to call some of these complex human skills "imitation." However, they clearly fit the evolutionary algorithm. Information is copied from person to person. Variation is introduced both by degradation, due to failures of human memory and communication, and by the creative recombination of different memes. And selection is imposed by limitations on time, transmission rates, memory, and other kinds of storage space. In this article, I am not going to deal with these more complex kinds of replication. Although they raise many interesting questions, they can undoubtedly sustain an evolutionary process and can, therefore, replicate memes. Instead I want to concentrate on skills at the simpler end of the scale , where it is not so obvious which kinds of learning can and cannot count as replicating memes.

Theories of gene-culture coevolution all differ in the ways their cultural units are supposed to be passed on. Cavalli-Sforza and Feldman's (1981) cultural traits are passed on by imprinting, conditioning, observation, imitation, or direct teaching. Durham's (1991) coevolutionary model refers to both imitation and learning. Runciman (1998) refers to memes as instructions affecting phenotype passed on by both imitation and learning. Laland and Odling Smee (2000) argue that all forms of social learning are potentially capable of propagating memes. Among meme-theorists both Brodie (1996) and Ball (1984) include all conditioning, and Gabora (1997) counts all mental representations as memes regardless of how they are acquired.

This should not, I suggest, be just a matter of preference. Rather, we must ask which kinds of learning can and cannot copy information from one individual to another in such a way as to sustain an evolutionary process. For if information is not copied through successive replications, with variation and selection, then there is no new evolutionary process and no need for the concept of the meme as replicator. This is not a familiar way of comparing different types of learning so I will need to review some of the literature and try to extract an answer.

Communication and Contagion

Confusion is sometimes caused over the term ‘‘communication,’’ so I just want to point out that most forms of animal communication (even the most subtle and complex) do not involve the copying of skills or behaviors from one individual to another with variation and selection. For example, when bees dance, information about the location of food is accurately conveyed and the observing bees go off to find it, but the dance itself is not copied or passed on. So this is not copying a meme. Similarly, when vervet monkeys use several different signals to warn conspecifics of different kinds of predator (Cheney & Seyfarth, 1990), there is no copying of the behavior. The behavior acts as a signal on which the other monkeys act, but they do not copy the signals with variation and selection.

Yawning, coughing, or laughter can spread contagiously from one individual to the next and this may appear to be memetic, but these are behaviors that were already known or in the animal's repertoire, and are triggered by another animal performing them (Provine, 1996). In this type of contagion, there is no copying of new behaviors (but note that there are many other kinds of contagion (Levy & Nail, 1993; Whiten & Ham, 1992)). Communication of these kinds is, therefore, not even potentially memetic. Various forms of animal learning may be.

Learning

Learning is commonly divided into individual and social learning. In individual learning (including classical conditioning, operant conditioning, acquisition of motor skills, and spatial learning), there is no copying of information from one animal to another. When a rat learns to press a lever for reward, or a cat learns where the food is kept, or a child learns how to ride a skateboard, that learning is done for the individual only and cannot be passed on. Arguably, such learning involves a replicator being copied and selected *within* the individual brain (Calvin, 1996; Edelman, 1989), but it does not involve copying *between* individuals. These types of learning, therefore, do not count as memetic transmission.

In social learning, a second individual is involved, but in various different roles. Types of social learning include goal emulation, stimulus enhancement, local enhancement, and true imitation. The question that I want to ask is which of these can and cannot sustain a new evolutionary process.

In emulation, or goal emulation, the learner observes another individual gaining some reward and, therefore, tries to obtain it too, using individual learning in the process, and possibly attaining the goal in quite a different way from the first individual (Tomasello, 1993). An example is when monkeys, apes, or birds observe each other getting food from novel containers, but then get it themselves by using a different technique (e.g., Whiten & Custance, 1996). This is social learning because two individuals are involved, but the second has only learned a new place to look for food. Nothing is copied from one animal to the other in such a way as to allow for the copying of variations and selective survival of some variants over others. So there is no new evolutionary process and no new replicator.

In stimulus enhancement, the attention of the learner is drawn to a particular object or feature of the environment by the behavior of another individual. This process is thought to account for the spread among British tits of the habit of pecking milk bottle tops to get at the cream underneath, which was first observed in 1921 and spread from village to village (Fisher & Hinde, 1949). Although this looks like imitation, it is possible that once one bird had learned the trick others were attracted to the jagged silver tops and they too discovered (by individual learning) that there was cream underneath (Sherry & Galef, 1984). If so, the birds had not learned a new skill from each other (they already knew how to peck), but only a new stimulus at which to peck. Similarly, the spread of termite fishing among chimpanzees might be accounted for by stimulus enhancement as youngsters follow their elders around and are exposed to the right kind of sticks in proximity to termite nests. They then learn by trial and error how to use the sticks.

In local enhancement, the learner is drawn to a place or situation by the behavior of another, as when rabbits learn from each other not to fear the edges of railway lines in spite of the noise of the trains. The spread of sweet-potato washing in Japanese macaques may have been through stimulus or local enhancement as the monkeys followed each other into the water and then discovered that washed food was preferable (Galef, 1992).

If this is the right explanation for the spread of these behaviors, we can see that there is no new evolutionary process and no new replicator, for there is nothing that is copied from individual to individual with variation and selection. This means there can be no cumulative selection of more effective variants. Similarly, Boyd and Richerson (2000) argue that this kind of social learning does not allow for cumulative cultural change.

Most of the population-specific behavioral traditions studied appear to be of this kind, including nesting sites, migration routes, songs, and tool use, in species such as wolves, elephants, monkeys, monarch butterflies, and many kinds of birds (Bonner, 1980). For example, oyster catchers use two different methods for opening mussels according to local tradition but the two methods do not compete in the same population—in other words there is no differential selection of variants within a given population. Tomasello, Kruger, and Ratner (1993) argue that many chimpanzee traditions are also of this type. Although the behaviors are learned population-specific traditions, they are not cultural in the human sense of that term because they are not learned by all or even most of the members of the group; they are learned very slowly and with wide individual variation, and—most telling—they do not show an accumulation of modifications over generations. That is, they do not show the cultural ''ratchet effect'' precluding the possibility of humanlike cultural traditions that have "histories.''

There may be exceptions to this. Whiten et al. (1999) have studied a wide variety of chimpanzee behaviors and have found limited evidence that such competition between variants does occur within the same group. For example, individuals in the same group use two different methods for catching ants on sticks and several ways of dealing with ectoparasites while grooming. They suggest that these require true imitation for their perpetuation.

Imitation

True imitation is more restrictively defined, although there is still no firm agreement about the definition (see Zentall, 1996; Whiten 1999). Thorndike (1898) originally defined imitation as ''learning to do an act from seeing it done.'' This means that one animal must acquire a novel behavior from another—so ruling out the kinds of contagion noted above. Whiten and Ham (1992), whose definition is widely used, define imitation as learning some part of the form of a behavior from another individual. Similarly, Heyes (1993) distinguishes between true imitation—learning something about the form of behavior through observing others, from social learning—learning about the environment through observing others (thus ruling out stimulus and local enhancement).

True imitation is much rarer than individual learning and other forms of social learning. Humans are extremely good at imitation; starting almost from birth and taking pleasure in doing it. Meltzoff, who has studied imitation in infants for more than 20 years, calls humans the consummate imitative generalist (Meltzoff, 1996) (although some of the earliest behaviors he studies, such as tongue protrusion, might arguably be called contagion rather than true imitation). Just how rare imitation is has not been answered. There is no doubt that some songbirds learn their songs by imitation, and that dolphins are capable of imitating sounds as well as actions (Bauer & Johnson, 1994; Reiss & McCowan, 1993). There is evidence of imitation in the grey parrot and harbour seals. However, there is much dispute over the abilities of nonhuman primates and other mammals such as rats and elephants (see Byrne & Russon, 1998; Heyes & Galef, 1996, Tomasello et al., 1993, Whiten, 1999).

Many experiments have been done on imitation and although they have not directly addressed the question of whether a new replicator is involved, they may help towards an answer. For example, some studies have tried to find out how much of the form of a behavior is copied by different animals and children. In the two-action method a demonstrator uses one of two possible methods for achieving a goal (such as opening a specially designed container), while the learner is observed to see which method is used (Whiten et al. 1996; Zentall, 1996). If a different method is used the animal may be using goal emulation, but if the same method is copied then true imitation is involved. Evidence of true imitation has been claimed using this method in budgerigars, pigeons, and rats, as well as enculturated chimpanzees and children (Heyes & Galef, 1996). Capuchin monkeys have recently been found to show limited ability to copy the demonstrated method (Custance, Whiten, & Fredman, 1999).

Other studies explore whether learners can copy a sequence of actions and their hierarchical structure (Whiten, 1999). Byrne and Russon (1998) distinguish action level imitation (in which a sequence of actions is copied in detail) from program level imitation (in which the subroutine structure and hierarchical layout of a behavioral program are copied). They argue that other great apes may be capable of program level imitation, although humans have a much greater hierarchical depth. Such studies are important for understanding imitation, but they do not directly address the question at issue here—that is, does the imitation entail an evolutionary process? Is there a new replicator involved?

To answer this, we need new kinds of research directed at finding out whether a new evolutionary process is involved when imitation, or other kinds of social learning, take place. This might take two forms. First, there is the question of copying fidelity. As we have seen, a replicator is defined as an entity that passes on its structure largely intact in successive replications. So we need to ask whether the behavior or information is passed on largely intact through several replications. For example, in the wild, is there evidence of tool use, grooming techniques, or other socially learned behaviors being passed on through a series of individuals, rather than several animals learning from one individual but never passing the skill on again? In experimental situations, one animal could observed another, and then act as model for a third, and so on (as in the game of Chinese whispers or telephone). We might not expect copying fidelity to be very high, but unless the skill is recognizably passed on through more than one replication, then one does not have a new replicator—i.e., there is no need for the concept of the meme.

Second, is there variation and selection? The examples gives by Whiten et al. (1999) suggest that there can be. We might look for other examples where skills are passed to several individuals; these individuals differ in the precise way they carry out the skill and some variants are more frequently or reliably passed on again. For this is the basis of cumulative culture. Experiments could be designed to detect the same process occurring in artificial situations. Such studies would enable us to say just which processes, in which species, are capable of sustaining an evolutionary process with a new replicator. Only when this is found can we usefully apply the concept of the meme.

If such studies were done and it turned out that by and large, what we have chosen to call imitation can sustain cumulative evolution, while other kinds of social learning cannot, then one could easily tie the definitions of memes and imitation together—so that what counts as a meme is anything passed on by imitation, and wherever you have imitation you have a meme.

In the absence of such research, we may not be justified in taking this step, and some people may feel that it would not do justice to our present understanding of imitation. Nevertheless, for the purposes of this paper at least, that is what I propose. The advantage is that it allows me to use one word "imitation" to describe a process by which memes are transmitted. If you prefer, for imitation, read "a kind of social learning which is capable of sustaining an evolutionary process with a new replicator."

This allows me to draw the following conclusion. Imitation is restricted to very few species and humans appear to be alone in being able to imitate a very wide range of sounds and behaviors. This capacity for widespread generalized imitation must have arisen at some time in evolutionary history. When it did so, a new replicator was created and the process of memetic evolution began. This, I suggest, was a crucial turning point in human evolution. I now want to explore the consequences of this transition and some of the coevolutionary processes that may have occurred once human evolution was driven by two replicators rather than one. One consequence, I suggest, was a rapid increase in brain size.

THE BIG HUMAN BRAIN

Humans have abilities that seem out of line with our supposed evolutionary past as hunter-gatherers, such as music and art, science and mathematics, playing chess, and arguing about our evolutionary origins. As Cronin puts it, we have a brain "surplus to requirements, surplus to adaptive needs" (Cronin, 1991, p. 355). This problem led Wallace to argue, against Darwin, that humans alone have a God-given intellectual and spiritual nature (see Cronin, 1991). Williams (1966) also struggled with the problem of "man's cerebral hypertrophy," unwilling to accept that advanced mental capacities have ever been directly favored by selection or that geniuses leave more children.

Humans have an encephalization quotient of about 3 relative to other primates. That is, our brains are roughly three times as large when adjusted for body weight (Jerison, 1973). The increase probably began about 2.5 million years ago in the australophithecines, and was completed about 100,000 years ago by which time all living hominids had brains about the same size as ours (Leakey, 1994; Wills, 1993). Not only is the brain much bigger than it was, but it appears to have been drastically reorganized during what is, in evolutionary terms, a relatively short time (Deacon, 1997). The correlates of brain size and structure have been studied in many species and are complex and not well understood (Harvey & Krebs, 1990). Nevertheless, the human brain stands out. The problem is serious because of the very high cost (in energy terms) of both producing a large brain during development, and of running it in the adult, as well as the dangers entailed in giving birth. Pinker asks "Why would evolution ever have selected for sheer bigness of brain, that bulbous, metabolically greedy organ? . . . Any selection on brain size itself would surely have favored the pinhead." (1994, p. 363).

Early theories to explain the big brain focused on hunting and foraging skills, but predictions have not generally held up, and more recent theories have emphasized the complexity and demands of the social environment (Barton & Dunbar, 1997). Chimpanzees live in complex social groups and it seems likely that our common ancestors did too. Making and breaking alliances, remembering who is who to maintain reciprocal altruism, and outwitting others, all require complex and fast decision-making and good memory. The ''Machiavellian Hypothesis'' emphasizes the importance of deception and scheming in social life and suggests that much of human intelligence has social origins (Byrne & Whiten, 1988; Whiten & Byrne, 1997). Other theories emphasise the role of language (Deacon, 1997, Dunbar, 1996).

There are three main differences between this theory and previous ones. First, this theory entails a definite turning point—the advent of true imitation that created a new replicator. On the one hand, this distinguishes it from theories of continuous change such as those based on improving hunting or gathering skills, or on the importance of social skills and Machiavellian intelligence. On the other hand, it is distinct from those that propose a different turning point, such as Donald's (1991) three-stage coevolutionary model or Deacon's (1997) suggestion that the turning point was when our ancestors crossed the ''symbolic threshold.''

Second, both Donald and Deacon emphasize the importance of symbolism or mental representations in human evolution. Other theories also assume that what makes human culture so special is its symbolic nature. This emphasis on symbolism and representation is unnecessary in the theory proposed here. Whether behaviors acquired by imitation (i.e., memes) can be said to represent or symbolize anything is entirely irrelevant to their role as replicators. All that matters is whether they are replicated or not.

Third, the theory has no place for the leash metaphor of sociobiology, or for the assumption, common to almost all versions of gene-culture coevolution, that the ultimate arbiter is inclusive fitness (i.e., benefit to genes). In this theory, there are two replicators, and the relationships between them can be cooperative, competitive, or anything in between. Most important is that memes compete with other memes and produce memetic evolution, the results of which then affect the selection of genes. On this theory, we can only understand the factors affecting gene selection when we understand their interaction with memetic selection.

In outline, the theory is this. The turning point in hominid evolution was when our ancestors began to imitate each other, releasing a new replicator, the meme. Memes then changed the environment in which genes were selected, and the direction of change was determined by the outcome of memetic selection. Among the many consequences of this change was that the human brain and vocal tract were restructured to make them better at replicating the successful memes.

THE ORIGINS OF IMITATION

We do not know when and how imitation originated. In one way, it is easy to see why natural selection would have favored social learning. It is a way of stealing the products of someone else's learning—i.e., avoiding the costs and risks associated with individual learning—though at the risk of acquiring outdated or inappropriate skills. Mathematical modelling has shown that this is worthwhile if the environment is variable but does not change too fast (Richerson & Boyd, 1992). Similar analyses have been used in economics to compare the value of costly individual decision-making against cheap imitation (Conlisk, 1980).

As we have seen, other forms of social learning are fairly widespread, but true imitation occurs in only a few species. Moore (1996) compares imitation in parrots, great apes, and dolphins and concludes that they are not homologous and that imitation must have evolved independently at least three times. In birds, imitation probably evolved out of song mimicry, but in humans it did not. We can only speculate about what the precursors to human imitation may have been, but likely candidates include general intelligence and problem-solving ability, the beginnings of a theory of mind or perspective-taking, reciprocal altruism (which often involves strategies like tit-for-tat that entail copying what the other person does), and the ability to map observed actions onto one's own.

The latter sounds very difficult to achieve—involving transforming the visual input of a seen action from one perspective into the motor instructions for performing a similar action oneself. However, mirror neurons in monkey premotor cortex appear to belong to a system that does just this. The same neurons fire when the monkey performs a goal-directed action itself as when it sees another monkey perform the same action, though Gallese and Goldman (1998) believe this system evolved for predicting the goals and future actions of others, rather than for imitation. Given that mirror neurons occur in monkeys, it seems likely that our ancestors would have had them, making the transition to true imitation more likely.

We also do not know when the transition occurred. The first obvious signs of imitation are the stone tools made by *Homo habilis* about 2.5 million years ago, although their form did not change very much for another million years. It seems likely that less durable tools were made before then, possibly carrying baskets, slings, wooden tools, and so on. Even before that our ancestors may have imitated ways of carrying food, catching game, or other behaviors. By the time these copied bahaviors were widespread, the stage was set for memes to start driving genes. I shall take a simple example and try to explain how the process might work.

MEMETIC DRIVE

Let us imagine that a new skill begins to spread by imitation. This might be, for example, a new way of making a basket to carry food. The innovation arose from a previous basket type, and because the new basket holds slightly more fruit it is preferable. Other people start copying it and the behavior and artifact both spread. Note that I have deliberately chosen a simple meme (or small memeplex) to illustrate the principle; that is, the baskets and the skills entailed in making them. In practice there would be complex interactions with other memes, but I want to begin simply.

Now anyone who does not have access to the new type of basket is at a survival disadvantage. A way to get the baskets is to imitate other people who can make them, and, therefore, good imitators are at an advantage (genetically). This means that the ability to imitate will spread. If we assume that imitation is a difficult skill (as indeed it seems to be) and requires a slightly larger brain, then this process alone can already produce an increase in brain size. This first step really amounts to no more than saying that imitation was selected for because it provides a survival advantage, and once the products of imitation spread, then imitation itself becomes ever more necessary for survival. This argument is a version of the Baldwin effect (1896), which applies to any kind of learning—once some individuals become able to learn something, those who cannot are disadvantaged and genes for the ability to learn, therefore, spread. So this is not specifically a memetic argument.

However, the presence of memes changes the pressures on genes in new ways. The reason is that memes are also replicators undergoing selection and as soon as there are sufficient memes around to set up memetic competition, then meme-gene coevolution begins. Let us suppose that there are a dozen different basket types around that compete with each other. Now it is important for any individual to choose the right basket to copy, but which is that? Since both genes and memes are involved we need to look at the question from both points of view.

From the genes' point of view, the right decision is the basket that increases inclusive fitness—i.e., the decision that improves the survival chances of all the genes of the person making the choice. This will probably be the biggest, strongest, or easiest basket to make. People who copy this basket will gather more food, and, ultimately, be more likely to pass on the genes that were involved in helping them imitate that particular basket. In this way, the genes, at least to some extent, track changes in the memes.

From the memes' point of view, the right decision is the one that benefits the basket memes themselves. These memes spread whenever they get the chance, and their chances are affected by the imitation skills, the perceptual systems, and the memory capacities (among other things) of the people who do the copying. Now, let us suppose that the genetic tracking has produced people who tend to imitate the biggest baskets, because over a sufficiently long period of time larger artifacts were associated with higher biological success. This now allows for the memetic evolution of all sorts of new baskets that exploit that tendency, especially baskets that look big. They need not actually be big, or well made, or very good at doing their job, but as long as they trigger the genetically acquired tendency to copy big baskets then they will do well, regardless of their consequence for inclusive fitness. The same argument would apply if the tendency was to copy flashy looking baskets, solid baskets, or whatever. So baskets that exploit the current copying tendencies spread at the expense of those that do not.

This memetic evolution now changes the situation for the genes which have, as it were, been cheated and are no longer effectively tracking the memetic change. Now the biological survivors will be the people who copy whatever it is about the current baskets that actually predicts biological success. This might be some other feature such as the materials used, strength, kind of handle, or whatever—and so the process goes on. This process is not quite the same as traditional gene-culture evolution or the Baldwin effect. The baskets are not just aspects of culture that have appeared by accident and may or may not be maladaptive for the genes of their carriers. They are evolving systems in their own right, with replicators whose selfish interests play a role in the outcome.

I have deliberately chosen a rather trivial example to make the process clear; the effects are far more contentious, as we shall see, when they concern the copying of language or of seriously detrimental activities.

Whom to Imitate

Another strategy for genes might be to constrain whom, rather than what, is copied. For example, a good strategy would be to copy the biologically successful. People who tended, other things being equal, to copy those of their acquaintances who had the most food, the best dwelling space, or the most children would, by and large, copy the memes that contributed to that success and so be more likely to succeed themselves. If there were genetic variation such that some people more often copied their biologically successful neighbors, then their genes would spread and the strategy "copy the most successful" would, genetically, spread through the population. In this situation (as I have suggested above), success and status is largely a matter of being able to acquire the currently important memes. So this strategy amounts to copying the best imitators. I shall call these people meme fountains, a term suggested by Dennett (1998) to refer to those who are especially good at imitation and who therefore provide a plentiful source of memes—both old memes they have copied and new memes they have invented by building on, or combining, the old.

Now we can look again from the memes' point of view. Any memes that got into the repertoire of a meme fountain would thrive, regardless of their biological effect. The meme fountain acquires all the most useful tools, hunting skills, fire-making abilities, and his genes do well. However, his outstanding imitation ability means that he copies and adapts all sorts of other memes as well. These might include rain dances, fancy clothes, body decoration, burial rites, or any number of other habits that may not contribute to his genetic fitness. Since many of his neighbors have the genetically in-built tendency to copy him, these memes will spread just as well as the ones that actually aid survival.

Whole memetic lineages of body decoration or dancing might evolve from such a starting point. Taking dance as an example, people will copy various competing dances and some dances will be copied more often than others. This memetic success may depend on whom is copied, but also on features of the dances, such as memorability, visibility, interest, and so on—features that in turn depend on the visual systems and memories of the people doing the imitation. As new dances spread to many people, they open up new niches for further variations on dancing to evolve. Any of these memes that get their hosts to spend lots of time dancing will do better, and so if there is no check on the process, people will find themselves dancing more and more.

Switching back to the genes' point of view, the problem is that dancing is costly in terms of time and energy. Dancing cannot now be unevolved but its further evolution will necessarily be constrained. Someone who could better discriminate between the useful memes and the energy-wasting memes would leave more descendants than someone who could not. So the pressure is on to make more and more refined discriminations about what and whom to imitate. And, crucially, the discriminations that have to be made depend upon the past history of memetic as well as genetic evolution. If dancing had never evolved, there would be no need for genes that selectively screened out too much dance imitation. Since it did, there is. This is the crux of the process called memetic driving. The past history of memetic evolution affects the direction that genes must take to maximize their own survival.

We now have a coevolutionary process between two quite different replicators that are closely bound together. To maximize their success, the genes need to build brains that are capable of selectively copying the most useful memes, while not copying the useless, costly, or harmful ones. To maximize their success, the memes must exploit the brain's copying machinery in any way they can, regardless of the effects on the genes. The result is a mass of evolving memes, some of which have thrived because they are useful to the genes, and some of which have thrived in spite of the fact that they are not—and a brain that is designed to do the job of selecting which memes are copied and which are not. This is the big human brain. Its function is selective imitation and its design is the product of a long history of meme-gene coevolution.

Whom to Mate With

There is another twist to this argument—sexual selection for the ability to imitate. In general, it will benefit females to mate with successful males and, in this imagined human past, successful males are those who are best at imitating the currently important memes. Sexual selection might, therefore, amplify the effects of memetic drive. A runaway process I have of sexual selection could then take off.

For example, let us suppose that at some particular time the most successful males were the meme fountains. Their biological success depended on their ability to copy the best tools or fire-making skills, but their general imitation ability also meant that they wore the most flamboyant clothes, painted the most detailed paintings, or hummed the favorite tunes. In this situation, mating with a good painter would be advantageous. Females who chose good painters would begin to increase in the population and this, in turn, would give the good painters another advantage, quite separate from their original biological advantage. That is, with female choice now favoring good painters, the offspring of good painters would be more likely to be chosen by females and so have offspring themselves. This is the crux of runaway sexual selection and we can see how it might have built on prior memetic evolution.

Miller (1998, 1999) has proposed that artistic ability and creativity have been sexually selected as courtship displays to attract women, and has provided many examples, citing evidence that musicians and artists are predominantly male and at their most productive during young adulthood. However, there are differences between his theory and the one proposed here. He does not explain how or why the process might have begun, whereas with this theory the conditions were created by the advent of imitation and, hence, of memetic evolution. Also with his theory the songs, dances, or books act as display in sexual selection, but the competition between them is not an important part of the process. With the theory proposed here, memes compete with each other to be copied by both males and females, and the outcome of that competition determines the direction taken both by the evolution of the memes and the brains that copy them.

Whether this process has occurred or not is an empirical question. But note that I have sometimes been misunderstood as basing my entire argument on sexual selection of good imitators (Aunger, 2000). In fact, the more fundamental process of memetic drive might operate with or without the additional effects of sexual selection.

THE COEVOLUTION OF REPLICATORS WITH THEIR REPLICATION MACHINERY

Memetic driving of brain design can be seen as an example of a more general evolutionary process—that is, the coevolution of a replicator along with the machinery for its replication. The mechanism is straightforward. As an example, imagine a chemical soup in which different replicators occur, some together with coenzymes or other replicating machinery, and some without. Those that produce the most numerous and long-lived copies of themselves will swamp out the rest, and if this depends on being associated with better copying machinery, then both the replicator and the machinery will thrive.

Something like this presumably happened on earth long before RNA and DNA all but eliminated any competitors (Maynard-Smith & Szathmary, 1995). DNA's cellular copying machinery is now so accurate and reliable that we tend to forget that it must have evolved from something simpler. Memes have not had this long history behind them. The new replicator is, as Dawkins (1976, p. 192) puts it, "still drifting clumsily about in its primeval soup ... the soup of human culture." Nevertheless, we see the same general process happening as we may assume once happened with genes. That is, memes and the machinery for copying them are improving together.

The big brain is just the first step. There have been many others. In each case, high quality memes outperform lower quality memes and their predominance favors the survival of the machinery that copies them. This focuses attention on the question of what constitutes high-quality memes. Dawkins (1976) suggested fidelity, fecundity, and longevity.

This is the basis for my argument about the origins of language (Blackmore, 2000). In outline it is this. Language is a good way of creating memes with high fecundity and fidelity. Sound carries better than visual stimuli to several people at once. Sounds digitized into words can be copied with higher fidelity than continuously varying sounds. Sounds using word order open up more niches for memes to occupy and so on. In a community of people copying sounds from each other, memetic evolution will ensure that the higher quality sounds survive. Memetic driving then favors brains and voices that are best at copying those memes. This is why our brains and bodies became adapted for producing language. With this theory, the function of language ability is not primarily biological but memetic. The copying machinery evolved along with the memes it copies.

The same argument explains why our brains seem especially adapted to soaking up some kinds of memes rather than others. For example, most people find mathematics and reading difficult, but adopting religious rituals, retelling stories, and singing songs easy. This argument parallels an important argument in evolutionary psychology. It has become increasingly clear that the human brain is not a general-purpose learning device, but is adapted to learn some things more readily than others, based on genetic advantage in past environments (Pinker, 1997; Tooby & Cosmides, 1992). The equivalent for memes is that the brain is not a general-purpose imitation machine, but one honed by memetic and genetic evolution to be good at copying some kinds of memes and bad at others. Songs, stories, and rituals have long taken part in gene-meme coevolution, while math and reading are relative newcomers, using machinery that was not designed for them.

These newcomers have brought with them further opportunities for the improvement of memes, and with that further steps in the design of replicating machinery—but this time outside of the brain. Writing improved the longevity of language memes and ensured the success of slates, pens, pencils, and libraries. Printing improved fecundity, and the spread of printed books ensured the survival of printing presses, factories, and bookshops. Communications by road, rail, ship, and aircraft served to spread more memes faster and they, in turn, encouraged the creation of even better means of travel.

We can see this process happening very fast now as communication technologies improve. The mobile phone is a good example. A decade ago few people would have predicted its phenomenal penetration. From the preserve of rich business people, it has become a commonplace teenage accessory. Why? Biological advantage is hardly relevant, and benefit to the individual is arguable when mobile phones reduce privacy and increase stress and noise pollution. From the memes' point of view, it makes perfect sense. With a mobile phone, people can transmit more memes than with a phone tied to one place. As these memes spread, they carry with them the idea of using the mobile phone, which thrives along with the memes it transmits. This suggests the testable prediction that the success or failure of new technologies is closely correlated with their effectiveness as meme-spreading devices.

Another general principle is the shift from what I have called "copy-the-product" to "copy-the-instruction" (Blackmore, 1999). In terms of fidelity, fecundity, and longevity it is preferable to copy the instructions for making something rather than copying the product itself. Copying a product (like a wheel, dance, or verbal story) inevitably allows for the introduction of errors (as in the soup discussed above) and those errors are cumulative over sequential copying. Higher fidelity copying is, therefore, achieved by copying the instructions, especially if they can be easily copied and safely stored. In this case, any errors made in building the product affect only one product and not a whole lineage. A further reduction in error rates can be achieved by digitizing the instructions. As Dawkins (1995) points out, this is why digital codes have evolved in both biology (in the form of the digital genetic code) and in human technologies such as telephones, hi-fi systems, and computers.

Copying the instructions also leads to higher fecundity because the same set of instructions can be used again and again. Finally, many products are necessarily ephemeral, such as soups, songs, music and, speech, but the instructions for making them can potentially be stored forever (whether in human memory or in cultural artifacts).

This suggests that copying the instructions is a better evolutionary strategy. In fact, this is an empirical issue that at least in limited domains, could be tested. But, assuming it is correct, we ought to find a shift from one mode of copying to the other throughout evolution, as the products of the better system outperformed those of the inferior system. This could be why we now find in biology the distinction into genotype and phenotype, and why "Lamarckian" inheritance does not occur in sexually reproducing species.

Many human inventions can be seen as shifts from copy-the-product to copy-the-instruction. For example, writing made it possible to recreate the same stories, myths, and social contracts again and again from the same stored instructions. Printing made possible the storage of type that could be used to produce multiple copies of the same book. More recently, high technology products are produced with enormous accuracy from instructions for building them we one see the appearance of systems that look very much like genotypes and phenotypes. For example, the instructions for storing and displaying text in the program

Word 97 are faithfully copied every time it is installed in a new computer (even if they do not always perform identically), but it is the products made by users (letters, books, and so on) that act like phenotypes or interactors in that their success determines how many more copies of Word 97 are made.

All these are examples of a powerful and general evolutionary principle. Higher quality replicators spread at the expense of poorer quality competitors, and as they do so, they spread the replication machinery that copied them. Most simply put, we have coevolution between replicators and their copying machinery. Not only is this how technology evolves, it is how we humans got our brains.

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