Grist and mills: on the cultural origins of cultural learning

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Page 1 of 34

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GRIST AND MILLS:

ON THE CULTURAL ORIGINS OF CULTURAL LEARNING

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1

ABSTRACT

Cumulative cultural evolution is what 'makes us odd'; our capacity to learn facts and techniques

from others, and to refine them over generations, plays a major role in making human minds and

lives radically different from those of other animals. In this article I discuss cognitive processes that

are known collectively as 'cultural learning' because they enable cumulative cultural evolution.

These cognitive processes include reading, social learning, imitation, teaching, social motivation, and

theory of mind. Taking the first of these three types of cultural learning as examples, I ask whether

and to what extent these cognitive processes have been adapted genetically or culturally to enable

cumulative cultural evolution. I find that recent empirical work in comparative psychology,

developmental psychology and cognitive neuroscience provides surprisingly little evidence of genetic

adaptation, and ample evidence of cultural adaptation. This raises the possibility that it is not only

'grist' but also 'mills' that are culturally inherited; through social interaction in the course of

development, we not only acquire facts about the world and how to deal with it (grist), we also build

the cognitive processes that make 'fact inheritance' possible (mills).

I. INTRODUCTION

The term *cultural learning* has been used increasingly in the last 20 years to refer to a broadly

defined group of psychological processes, such as reading, social learning, imitation, teaching, social

motivation, and theory of mind (1). They are known collectively as cultural learning, or *cultural*

cognition (2), because they are thought to enable cumulative cultural evolution, i.e. the non-genetic

inheritance of information in a way that allows individual and group phenotypes to achieve a

progressively better fit with the demands of the social and physical environment (Laland & Lewis (3),

this issue; Shea (4), this issue). Many researchers interested in the evolution of human cognition

believe that this kind of cultural inheritance is what "makes us odd" (5). It is what makes the lives of

contemporary humans – with our built environment, science, technology, art, political and economic

systems – so very different from the lives of other animals, including those of our closest living

relatives.

         This article concerns the origins of cultural learning. Do the different types of cultural

learning just happen to be able to support cultural inheritance, or have they been adapted to fulfil

this function? If they have been adapted for cultural inheritance, to what extent have the

adaptations been produced by genetic and by cultural processes? Researchers from the Santa

Barbara school of evolutionary psychology assume that cultural learning is made possible by genetic

adaptations; by an array of 'innate modules' or 'instincts' selected specifically for their capacity to

support cultural inheritance (6, 7). Even researchers who typically eschew nativism, and emphasise

the power of cultural evolution, sometimes imply that the capacity for cultural learning is inborn (5)

(8). For example, Tomasello & Herrmann suggest that "..human children come into the world ready

to 'collaborate', as it were, with forebears in their culture, by adopting their artifacts, symbols, skills,

and practices via imitation and instructed learning" (8).

         The idea that cultural evolution is made possible by genetic or 'biological' adaptations for

cultural learning is both simple and plausible. It suggests a straightforward rooting of cultural

3

evolution in biological evolution, and makes the reasonable assumption that there would have been selection pressure in favour of cognitive processes that enable cumulative cultural evolution. However, in this article I review recent research in comparative psychology, developmental psychology and cognitive neuroscience indicating that there is surprisingly little evidence that cultural learning is based on cognitive mechanisms that have been genetically adapted specifically to enable the social transmission of information. No doubt, like nearly all complex phenotypic traits, the cognitive mechanisms of cultural learning are at some level genetic adaptations; they have been shaped by natural selection to fulfil some function(s); for example, to enable learning about predictive relationships between events, or to support precise visuomotor control. But there is very little evidence that they are genetic adaptations *for* cultural learning – that they have been shaped by natural selection specifically to enable the social transmission of information.

Instead I propose that the specialised features of cultural learning – the features that make cultural learning especially good at enabling the social transmission of information – are acquired in the course of development through social interaction. This implies that the cognitive processes that comprise cultural learning are themselves culturally inherited; they are cultural adaptations. They are products as well as producers of cultural evolution. We tend to assume that 'grist' – facts about the world, and techniques for dealing with the world – are culturally inherited, and that this is made possible by genetically inherited 'mills' – psychological processes that enable us to learn the grist from others. In contrast, the 'new thinking' in this article proposes that it is not only the grist but also the mills that are culturally inherited; that the mechanisms of cultural learning are forged and transmitted through social interaction.

The article focusses on three examples of cultural learning: reading (or literacy), social learning, and imitation. I have chosen reading because it provides a relatively unambiguous example of the cultural inheritance of cultural learning - a proof of principle. Social learning makes an interesting contrast with reading because it is heterogeneous, not uniquely human, and highlights a psychologically important distinction between *core mechanisms* of learning, and perceptual,

4

attentional and motivational *input mechanisms* (9). Imitation is an especially telling example

because it is widely regarded as a uniquely human adaptation for cultural inheritance, and yet recent

research suggests that the capacity to imitate is socially constructed in the course of development.

2. READING

No one doubts that reading is an immensely powerful form of cultural learning; a cognitive process

that enables those who are literate to access a huge store of information acquired by previous

generations. Furthermore, almost no one doubts that reading has been made possible by cultural

evolution. Written language emerged too recently in human history for there to be genetic

adaptations for reading. What is perhaps not so widely appreciated is the radical nature of the

changes that are wrought on the neurocognitive system by learning to read (10). This section

provides a brief overview of these changes. They remind us that social experience, like 'genes', can

have profound effects on the mind and brain. It can create whole new systems of thought; systems

that could easily be mistaken for innate modules.

Research on the psychological mechanisms involved in reading is informed by experiments

examining the speed of processing and the kinds of errors made during reading by healthy literate

people, and by people with various types of brain damage. According to one of the most prominent

models, the 'dual route cascaded model' (DRC) (11), the full corpus of data from these studies

implies that each competent reader has distinct psychological routes from seeing a letter string to

reading it aloud (see Figure 1). The *lexical semantic route* first goes from letters to a mental

dictionary of printed word forms (orthographic input lexicon), then to a semantic system encoding

word meanings, then to a phonological output lexicon, storing sound information relating to words,

and finally to the system producing spoken words. The *lexical non-semantic route* by-passes the

semantic system, but uses the orthographic input and phonological output lexicons. The *grapheme-

phoneme correspondence route* by-passes even these, allowing visually presented letters to activate

phonemes and to produce speech output directly. Each of these routes, and some of their

5

components (e.g. the orthographic input lexicon, the grapheme-phoneme rule system), are constructed by the process of learning to read. Even where a component – such as the phonological output lexicon or phoneme system – is in place prior to learning, route construction transforms the way in which it operates. Furthermore, these changes, wrought purely by education, affect the processing of spoken as well as written words.

Figure 1 about here

Some of the best evidence of these radical effects of learning to read comes from behavioural studies (12). However, the transforming effects of learning to read have been demonstrated most dramatically using brain imaging. A recent study (13) found that viewing written sentences activated large areas of the cortex more strongly in literate than in illiterate adults. These areas included: the right occipital cortex, which is involved in relatively low-level visual processing; the left perisylvian temporal and frontal language areas; and a focal area of the occipito-temporal cortex. The latter area is known as the *visual word form area* (VWFA) because it responds so reliably, in literate people, to the presentation of written words. If one did not know that reading is culturally inherited, it would be easy to mistake the robust response characteristics and precise localisation of the VWFA for signs that the capacity to read depends on an innate module. When the subjects in this imaging experiment listened to spoken words, literacy was associated with substantially greater activation in the planum temporally, an area involved in phonological coding, and in the occipito-temporal regions that analyse visual word forms. This is consistent with other evidence that learning to read restructures our representations of spoken words (14). After learning to read we segment spoken language into different units, and we not only hear, we also see, spoken words – they activate visual areas of the brain.

Thus, learning to read has major, constructive effects on the neurocognitive system. It does not, of course, create a new system from scratch. Like other biological and cultural processes of adaptation, learning to read takes old parts and remodels them into a new system (15).   The old parts are computational processes and cortical regions originally adapted, genetically and culturally,

6

for object recognition and spoken language, but it is an ontogenetic, cultural process – literacy

training – that makes them into a new system specialised for cultural learning.

The case of reading shows clearly that processes of cultural learning can be culturally

inherited. The largely unexplored question is – how far does this go? To what extent are other

processes of cultural learning also culturally inherited?

3. SOCIAL LEARNING

In pursuit of that question, let us turn to social learning. It is commonly claimed that social learning

is an important variety of cultural learning (5), but social learning is a very different case from

reading, in a number of respects. First, social learning is a generic and amorphous category. Agents

are said to have engaged in social learning when they have learned something by observing the

actions of another agent, or the products of those actions – but only if the model's actions were not

tailored to this end. If the model's behaviour was intended to communicate some information to

the observer, or has evolved genetically to do so, the phenomenon is typically called 'signalling' or

'teaching' rather than social learning. Second, it is well-known that other animals, not just humans,

engage in social learning. For example, rat pups learn what to eat by observing the dietary choices

of adults (16), and monkeys learn that snakes are dangerous by observing the fearful reactions of

conspecifics to snakes (17). This being so, it is clear that social learning is very far from sufficient for

cultural evolution. Otherwise a broad range of species would show human-like cultural inheritance.

However, as many authors have noted, social learning could be important for cultural evolution

without being sufficient (e.g. Laland & Lewis (3), this volume), and, as we shall see, the fact that

other animals are capable of social learning turns out to be very useful when we are asking about its

evolutionary origins. Finally, while virtually everyone agrees that reading is a product of cultural

evolution, it is widely assumed that social learning is mediated by computationally distinctive

psychological processes that have evolved through gene-based selection to facilitate the non-genetic

inheritance of information (18-20).

7

In contrast with this assumption, a review of recent evidence suggests that social learning does not involve special learning processes of either genetic or cultural origin (21). The *core mechanisms* of social learning – the 'digestive' processes that encode information for long-term storage - are the same associative mechanisms that encode information for long-term storage when it is derived, not from observing the behaviour of others (social learning), but from direct interaction with the inanimate world (asocial learning). What makes social learning distinctively 'social' is the way in which *input mechanisms* – perceptual, attentional and motivational processes that 'ingest' information for learning – are biased towards information from social sources. Crucially, there is evidence that in humans this biasing is often developmental; it occurs within lifetime and as a result of sociocultural experience. The next two sections summarise the evidence pointing to these conclusions.

Core mechanisms of social learning

Five lines of evidence suggest that social learning is mediated by the same core mechanisms of associative learning that allow humans and other animals to learn by direct interaction with the world. First, studies of birds and primates have shown that, across species (22, 23) and across individuals within a species (24, 25), asocial and social learning capabilities are positively correlated. Animals that are good at social learning are also good at asocial learning. Second, even solitary animals – such as the common octopus and the red-footed tortoise (20) – are capable of social learning. Third, the 'anatomy' of social learning is very similar to the anatomy of asocial learning; different types of social learning map onto different types of asocial learning (26). For example, specialists in the study of social learning distinguish *stimulus enhancement*, in which the model's activity exposes the observer to a single stimulus, from *observational conditioning*, in which the model's activity exposes the observer to a relationship between two stimuli. This corresponds to the distinction used by experts on associative learning between *single stimulus learning* (including phenomena such as sensitisation and habituation) and *stimulus-stimulus learning* or *Pavlovian*

Page 9 of 34

Submitted to Phil. Trans. R. Soc. B - Issue

1
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conditioning. Fourth, each type of social / associative learning is found in diverse species. For example, observational conditioning occurs in humans and in damselfly larvae. Human studies indicate that participants can learn an aversion to a stimulus such as a blue square not only as a result of experiencing electric shocks in the presence of the blue square (asocial learning / Pavlovian conditioning), but also by observing a model wince, as if in pain, in the presence of the blue square (social learning/observational conditioning) (27). Similarly, damselfly larvae learn to avoid pike, one of their predators, through exposure to pike stimuli (chemical cues in water) in conjunction with injured damselflies (28). Finally, each type of social learning bears the footprints of associative learning; it has operating characteristics known to be distinctive to associative learning. For example, observational conditioning shows blocking and overshadowing effects both when it is involved in the acquisition of dietary preferences by rats, and when it mediates fear learning in humans (27, 29).

These five lines of evidence suggest that, at the level of core psychological mechanisms, there is nothing 'special' about social learning. There is no need to ask whether the core mechanisms of social learning have been shaped by genetic or cultural evolution to promote the social transmission of information because there is no evidence that they have been adapted, by either means, to fulfil this function. However, this does not mean that there is nothing distinctive about social learning. In some cases, social learning is just learning that happens to be about events to which the individual has been exposed through social interaction. But in other cases there is evidence that input mechanisms – perceptual, attentional and motivational processes – have been adapted to make information from social sources especially salient or accessible. In principle this kind of adaptive biasing of input mechanisms could occur phylogenetically, under the influence of gene-based selection, or ontogenetically, via learning mechanisms and through social interaction.

9

Submitted to Phil. Trans. R. Soc. B - Issue

Page 10 of 34

Input mechanisms

A comprehensive survey will be necessary to establish whether adaptive biasing of input mechanisms towards social sources is predominantly phylogenetic or ontogenetic in humans. However, pending such a review, two recent studies suggest that ontogenetic processes are powerful and important.

The first study, by Behrens and colleagues (30), shows that input mechanisms can be biased towards (and away from) social sources by associative learning, and that this can happen flexibly on a relatively short time scale. In this experiment people were asked repeatedly to choose between a blue and a green option to earn points that would be later turned into money. At the beginning of each trial the options showed numbers. At some times in the experiment these gave a very accurate guide to how many points would be received if the subject selected the option, and at other times they were misleading. Next the subject was offered some advice – to choose blue or green - by an unseen confederate. Like the numbers, this social information was trustworthy in some phases and untrustworthy in others. At the end of each trial the subject made her choice, and was told how many points she was going to get on that trial. Modelling of choice behaviour, and of cortical blood oxygen dependent (BOLD) responses during task performance, showed that people used both sources of information, the numbers and the confederate's advice, in a broadly rational way. The weights assigned to the two sources – the extent to which each input was privileged in decision making - varied with the recent trustworthiness of the source, and how rapidly the trustworthiness of each source was currently changing. Modelling of the BOLD responses also showed that the value of each source of information was being tracked using prediction error, a computational mechanism characteristic of associative learning. Each time an outcome was observed, two areas of the brain – the ventral striatum (numbers) and the medial prefrontal cortex (advice) – were updating the value of the source using the difference between the outcome expected and that which was actually observed. Thus, this study by Behrens and colleagues shows that people rapidly and continuously

decide whether or not to take advice, and that this input modulation is mediated by associative

learning, i.e. processes that are genetically adapted, not for cultural learning specifically, but for

tracking predictive relationships between all kinds of events.

The second example of developmental biasing of input mechanisms shows that the bias can

be durable and very specific, promoting attention to a particular category of social stimuli. In this

study, Jack and colleagues (31) used eye movement tracking to measure attention to emotional

faces in Western Caucasian and East Asian participants. Across all emotion types and face

ethnicities, they found that Western Caucasians divided their attention more equally between the

eyes and mouth than the East Asians, who focussed more on the eyes. When they looked at each

emotion separately, and examined the accuracy with which the expressions were recognised, Jack et

al. found that the Western Caucasians' greater attention to the mouth area resulted in better

recognition of fear and disgust than in the East Asian participants. This kind of cultural tuning of

attention to social stimuli could have profound effects on social learning. For example,

observational conditioning is a primary means of learning the value or emotional valence of types of

object or event; people, animals, plants or practices become attractive or aversive when they are

paired with positive or negative expressions of emotion by others. Therefore, if Western Caucasians

are more sensitive to expressions of fear and disgust, it is likely that they would learn more readily

via observational conditioning that certain objects are threatening or repulsive. In this particular

domain they may be faster social learners, not because they have better or different genetic

adaptations for social learning, but as a result of sociocultural experience tuning input mechanisms

to a particular configuration of facial features.

In summary: Current evidence suggests that social learning does not involve learning

mechanisms that have been adapted – genetically or culturally – for cultural inheritance. However,

some examples of social learning are distinctively social in that they involve input mechanisms that

are biased towards information supplied by other agents. There is evidence from human and

nonhuman animals (21) that this biasing is itself a consequence of social learning; through

interaction with other agents in our group or culture, we learn to privilege input from certain social

sources – under specific conditions, or across contexts.

4. IMITATION

Imitation (or 'imitation learning') is a type of social learning that is thought to play an especially

important role in cultural inheritance (1, 5, 32, 33). It is social learning in which the observer

acquires new behavioural topography – a new way of moving parts of the body relative to one

another - by observing another agent. Noting that skills such as flint knapping and basket weaving

require new ways of moving the hands and fingers, relative to one another and to materials, many

researchers regard imitation as crucial for the cultural inheritance of instrumental-technological

skills. Imitation also appears to be indispensable in the development of communicative-gestural

skills, in learning the postures, gestures and ritualistic movement patterns – such as those used in

dance – that promote social bonding within groups and distinguish ingroup from outgroup members

(34).

Applying the distinction used in the previous section, the question whether imitation is

made possible by genetically evolved and/or culturally inherited cognitive mechanisms can be

broken down into two parts: what are the origins of 1) the core mechanisms of imitation, and 2) the

input processes that feed imitation.

Core mechanisms of imitation

It has long been assumed that imitation is made possible by genetically evolved and highly

specialised cognitive mechanisms (35); by what might now be described as an innate module. This is

plausible for three reasons. First, humans are *Homo imitans* (33); we may not be the only species

that can imitate, but the range and precision of our imitation of body movements (rather than

vocalisations) far outstrips anything found elsewhere in the animal kingdom. Second, imitation

makes some highly distinctive demands on the cognitive system, and it is tempting to assume that

specialised problems have specialised solutions. Unlike all other forms of social learning, and indeed

most other types of behaviour, imitation requires the cognitive system to solve the *correspondence*

problem (36); to translate observed actions into matching executed actions; action percepts into

corresponding motor programmes. Third, it is difficult to imagine how domain-general cognitive

processes could solve the correspondence problem, especially for actions such as facial expressions

and whole body movements, which look very different to me when I am doing them and when I am

watching you doing them. These three considerations have lent support to models suggesting,

implicitly or explicitly, that the core problem of imitation – the correspondence problem – is solved

by specialised, human-specific, innate mechanisms that were favoured by natural selection because

they enable cultural inheritance.

However, recent research has 'imagined' a way in which the correspondence problem could

be solved by domain-general cognitive processes, and provided evidence that it is, in fact, solved in

this domain-general way. The imagined solution is known as the associative sequence learning

model of imitation (ASL)(37, 38). If the ASL model is correct, the capacity to imitate is to a very

significant extent culturally inherited. The ASL model has two related advantages over the modular

view. First, rather than simply saying that there is a psychological 'black box' that makes imitation

possible, it specifies the cognitive mechanisms that solve the correspondence problem. Second,

through this specification the ASL model makes testable predictions about imitation that have been

confirmed by a now extensive body of experimental work. The remainder of this section gives an

outline of the ASL model, explains why it implies that imitation is culturally inherited, and surveys

some of the evidence supporting the model.

The ASL model suggests that imitation is made possible by direct, excitatory connections

between visual and motor representations of action; between 'mental images' of what an action

'looks like' and what it 'feels like' to perform the action (see Figure 2). These connections, or

matching vertical associations, are forged in the course of an individual's development by the same

domain- and species-general processes of associative learning that produce Pavlovian and

13

Submitted to Phil. Trans. R. Soc. B - Issue

Page 14 of 34

instrumental conditioning in the laboratory. When an observer copies a novel sequence of actions,

the operation of matching vertical associations is guided by domain-general processes that encode

the serial order of visual stimuli. These *horizontal* processes learn what the novel action sequence

looks like. The representation they construct would be sufficient for subsequent recognition of the

sequence, and to distinguish it from sequences containing the same components in a different

order. However, for imitation of a novel action – to turn vision into matching action - the visual

sequence representation formed by horizontal processes must activate, in the appropriate order, a

matching vertical association for each element of the sequence. Therefore, it is the vertical

associations – connecting visual and motor representations of the same action – that solve the

correspondence problem. They are the core mechanisms of imitation.

Figure 2 about here

Processes of associative learning strengthen excitatory connections between pairs of event

representations when the occurrence of the two events is correlated, i.e. when they occur relatively

close together in time (contiguity) and one event is predictive of the other (contingency). Therefore,

a matching vertical association for, say, finger splaying would be formed by experience in which the

sight of finger splaying is correlated with the performance of finger splaying. In terms of their

internal structure, the processes of associative learning could just as easily produce non-matching as

matching vertical associations. If the sight of one action, X, is correlated with the performance of a

different action, Y, associative learning will strengthen the connection between a visual

representation of X and a motor representation of Y, supporting counter-imitative rather than

imitative behaviour. The ASL model implies that matching vertical associations predominate, and

therefore that humans develop a capacity for imitation, rather than for counter-imitation, because

certain features of the human developmental environment ensure that we more often experience

correlations between observation and execution of the same action than of different actions. For

example, experience of the former kind comes from direct self-observation (e.g. looking at your own

14

hands in motion), mirror self-observation (using reflective surfaces), being imitated by others

(especially facial imitation of infants by adults), synchronous activities of the kind involved in dance,

sports and military training, and indirectly via the use of action words (39). Notice that nearly all of

these kinds of experience involve interaction with cultural artefacts (mirrors) or with other people in

culture-specific contexts. Even an infant's opportunity to look directly at her own hands in motion is

modulated by culture-specific childrearing practices such as swaddling. Therefore, the range of

actions for which an individual has matching vertical associations – the range of actions she is able to

imitate – depends on sociocultural experience and is culturally inherited along with artefacts,

practices, rituals and verbs.

Unlike previous accounts of the cognitive mechanisms mediating imitation, the ASL model

has been explicitly tested against alternative models. These experiments have examined the

imitation of familiar actions and of novel sequences of actions, using behavioural and

neurophysiological measures, and probing the model's hypotheses about both vertical and

horizontal processes (see (38) for a review). Supporting the idea that matching vertical associations

are forged by associative learning, these studies have shown that novel sensorimotor experience can

enhance (40), abolish (41) and even reverse (42, 43) simple imitative behaviour, and that these

effects depend on the contingency between observed and executed actions (44). It has been widely

reported that humans typically show 'automatic imitation' of various hand and foot movements: in

tasks that require us to ignore the sight of these movements, we nonetheless respond faster and

more accurately when the required action matches an observed body movement (45). Hand opening

is faster when observing hand opening than when observing hand closing, foot lifting is faster when

observing foot lifting than hand lifting, and so on. These imitative effects appear to be relatively

impervious to the actor's intentions, but they can be changed by retraining (45). For example,

without explicit training, passive observation of index finger movement activates muscles that move

the index finger more than muscles that move the little finger. However, after training in which

people were required to respond to index finger movements with little finger movements, and vice

15

versa, this pattern was reversed. Observation of index finger movement activated little finger

muscles more than index finger muscles, implying that associative learning had converted automatic

imitation into automatic counter-imitation (42, 43).

Similarly, experiments examining the imitation of novel sequences of actions have provided

evidence that it involves the same kind of sequence learning processes as non-imitative tasks; that

these processes do not depend on intention-reading (46); and that they do not show the flexibility

one would expect if imitation were mediated by dedicated mechanisms (47). For example, when

people are required to imitate a sequence of movements involving the selection of a pen and its

placement in one of two containers, they show exactly the same pattern of errors as when they are

instructed to perform the same movements by flashing geometric shapes. Error patterns are

indicative of underlying cognitive processes. Therefore these results indicate that the same

sequence encoding mechanisms are recruited in imitative and non-imitative tasks, and by stimuli

that do and do not support the attribution of intentions (46).

Two objections are commonly raised against the ASL model and its implication that the

capacity to imitate is culturally inherited. The first *poverty of the stimulus* objection suggests that

the ASL model must be wrong because there is evidence that newborn babies can imitate a range of

actions. This objection will be addressed only briefly here because it has been examined in detail in

a recent review (39). Building on previous analyses (48), this review found evidence that neonates

copy only one action – tongue protrusion – and that this copying does not show the specificity

characteristic of imitation (49). Figure 3 illustrates the first of these points. For each of the action

types tested in young infants, it shows the number of published studies reporting positive evidence

of imitation and the number reporting negative evidence. This is a highly conservative measure of

how often young infants have failed imitation tests because it is much harder to publish negative

than positive results. Nonetheless, Figure 3 shows that the number of positive reports substantially

exceeds the number of negative reports only for tongue protrusion. Evidence that even tongue

protrusion matching lacks the specificity characteristic of imitation comes from studies showing that

tongue protrusion can be elicited by a range of arousing stimuli, including flashing lights and lively

music (49).

Figure 3 about here

The second objection says that the ASL model may be a correct description of how the

capacity to imitate got off the ground, but not of the way in which the core mechanisms of imitation

develop in contemporary humans. Perhaps our ancestors started out by learning to imitate 'from

scratch' – without any inborn vertical associations for imitation, and using domain-general

associative mechanisms - but then the capacity to imitate proved to be so useful that there was

selection in favour of genetic mutations that *canalised (50)*, *prepared* (51) or *genetically assimilated*

(52) the learning of matching vertical associations. I will call this the *genetic assimilation* objection,

but really it is a family of objections because the mutations could have acted in a variety of ways.

They could have established stronger inborn connections between visual and motor representations

of the same actions than of different actions; enhanced the speed or probability of learning

matching, relative to nonmatching, vertical associations; or acted to preserve the functioning of

matching vertical associations once they have been established.

The first thing to note in relation to the genetic assimilation objection is that the ASL model

does not deny that some vertical associations may be inborn or easier to learn than others, and that

this could be due to genetic evolution. However, the ASL model suggests that any 'privileged'

associations of this kind are genetic adaptations for the visual guidance of action. Therefore, the ASL

model would be compatible with the discovery of, for example, stronger inborn connections

between visual representations of large objects and motor representations of power (rather than

precision) grips, but it would *not* be compatible with evidence of stronger inborn connections

between visual representations of power grips and motor representations of power (rather than

precision) grips. In other words, the ASL model naturally embraces the idea that imitation is based

17

on genetic adaptations – associative learning itself is a genetic adaptation – but it denies that these genetic adaptations are *for* imitation or any other aspect of social cognition.

The second thing to note about the genetic assimilation objection is that it points out a logical possibility; it does not advance any concrete evidence that the possibility has been realised. It is not based on evidence that matching vertical associations are inborn, easier to learn, or more resistant to change than nonmatching vertical associations. In contrast, as indicated above, the ASL model has generated novel predictions about imitation and those predictions have been confirmed in a range of experiments. For example, these experiments have shown that automatic imitation can be abolished and even reversed by relatively brief periods of novel sensorimotor training (40-42). This is what one would expect if both matching and nonmatching vertical associations are established via standard mechanisms of associative learning, and it provides no encouragement whatever for the view that the acquisition of matching vertical associations has been genetically assimilated for imitation (53).

Finally, a recent neuroimaging study of the *mirror neuron system* sought, and failed to find, evidence of even a relatively weak form of genetic assimilation; evidence that the learning that produces matching vertical associations is specialised or constrained to link sensory representations of action, rather than of inanimate stimuli, with motor representations (54). Mirror neurons are cells found in the premotor and parietal cortex of monkeys and humans that discharge when a certain type of action (e.g. power grip) is observed, and selectively when the same type of action is executed (55, 56). The ASL model suggests that each mirror neuron is the 'motor end' of a matching vertical association. The 'visual end' – the visual representation that has become linked with a matching motor representation – is typically located in the superior temporal sulcus, an area that specialises in the visual processing of biological movement (53). Press et al. looked for signs that mirror neurons are canalised or prepared to develop in this way - to represent correlations between observed and executed movements - or, as the ASL model predicts, whether they are plastic enough

18

to represent correlations involving geometric shapes. They found a striking degree of plasticity. A brief period of shape-action sensorimotor training was sufficient to create 'geometrical shape mirror neurons'; to link mirror neurons with visual neurons in parts of the brain that are not specialised for action processing. This kind and degree of plasticity is not what one would expect if the development of mirror neurons had been genetically assimilated for imitation or indeed any other social cognitive function.

To summarise: The ASL model is currently the most empirically successful description of the core mechanisms of imitation, of the neurocognitive processes that make imitation possible by solving the correspondence problem. This model suggests that associative learning and specified types of sociocultural experience convert a system which is genetically adapted for visuomotor control into a system that is culturally adapted for imitation.

Input mechanisms: Under- and over-imitation

The core mechanisms of imitation determine whether an agent *can*, but not whether she *will*, imitate an observed action. The core mechanisms make imitation possible, but in most cases this potential is not automatically translated into overt imitative action. Rather, the agent decides, consciously or unconsciously, whether to enact imitation, and like all decisions relating to voluntary action, this decision depends crucially on motivational processes; it depends on what the agent expects the outcome of imitation to be, and on the value she assigns to that outcome. Recent research on *under-imitation* and *over-imitation* in children has been interpreted as indicating that, even if the core mechanisms of imitation are not genetic adaptations, imitation involves motivational processes that have been shaped by genetic evolution to promote cultural inheritance. This is an interesting and wholly coherent hypothesis but it does not currently have clear empirical support. There is no reason to doubt that humans are better at all forms of cultural learning than other animals (57), or that enhanced social motivation is important in promoting human imitation,

19

but research on under- and over-imitation has not yet established that human social motivation has

been enhanced by genetic rather than cultural processes.

Under-imitation (or, as it is more commonly known, *rational imitation*) provides primary

support for the *natural pedagogy* hypothesis – the idea that human infants have genetic adaptations

making them sensitive to the teaching intentions of adults; to behavioural cues indicating what

adults want infants to learn (58). In the original study of under-imitation (59), 12- to 14-month-old

infants saw an adult switching on a light by touching the light with her forehead. When the adult did

this, her hands were occupied, holding a blanket around her body, or free, lying on either side of the

light box. When given access to the box themselves, infants who had seen hands occupied were less

likely to copy the head movement – they under-imitated – relative to infants who had seen hands

free. This was taken to indicate that the infants had worked out, using cognitive mechanisms

genetically adapted for natural pedagogy, that the adult had only used her head because her hands

were occupied, and, given that the infants were not similarly constrained, they could use their hands

instead. However, a recent study challenged this interpretation by suggesting that the infants who

saw hands occupied under-imitated simply because they were distracted by the blanket, and

therefore less likely than the hands free infants to notice that the adult used her head (60). This

study replicated the under-imitation effect found in the original study, but also included a group of

infants who were habituated to the sight of the blanket before seeing the hands occupied

demonstration. When the potential for distraction was removed in this way, the hands occupied

group was just as likely as the hands free group to copy the head action. Thus, the results of this

study undermine a major plank of the current evidence for natural pedagogy, and the component

that relates natural pedagogy most directly to imitation.

Over-imitation refers to children's tendency to imitate more components of an adult's action

than is strictly necessary to obtain the outcome achieved by the model. For example, Lyons et al.

allowed 3- to 5-year old children to observe an adult performing a four component sequence of

actions on a puzzle box, which terminated in the retrieval of a toy turtle from the box (61). The first

20

two components (using a wand to remove a bolt, and tapping the wand on the box) were causally

irrelevant; they were not necessary to get access to the toy. Nonetheless, these components were

imitated along with the causally relevant components, even when the children had been trained to

discriminate actions that they "had to do" from "silly" actions, and when they had been told "You

can get it out however you want".

There are many different hypotheses about what is going on in the minds of children during

over-imitation. The *causal hypotheses* see over-imitation primarily as a window on children's

developing understanding of causality, whereas the *social hypotheses* suggest that over-imitation

results from distinctively social motivation; the desire to be like adults, to share experiences with

others, to be liked by the model, and/or to uphold social norms (62). Assuming that social

motivation at least contributes to over-imitation, these social hypotheses raise the question of how

children come to be so highly socially motivated. Some discussions imply that heightened social

motivation is inborn, and that it is a genetic adaptation for cultural inheritance. This is certainly

possible, but the idea has not yet been tested systematically against the obvious alternative: in the

course of early development, children are reliably and richly rewarded by adult approval for

imitating a broad range of actions (63), and this not only contributes to the development of

matching vertical associations (see previous section), but also leaves children with the expectation

that imitative behaviour will be valued and therefore rewarded. Indeed, through an associative

process known as *higher order conditioning*, it could make imitating or agreeing with others (64),

rewarding in its own right. This hypothesis suggests that social motivation is culturally inherited;

infants acquire it through social interaction with adults because the adults are themselves socially

motivated. To test it against the idea that social motivation is a genetic adaptation for cultural

inheritance, one would need, for example, a full programme of transfer experiments in which

children are systematically rewarded or not rewarded for over-imitation in one set of tasks, and then

tested for over-imitation in a another set of tasks involving different adults and materials. In the

meantime, as this section has indicated, it is an open question to what extent the motivational

21

processes that guide imitative behaviour are genetically and/or culturally adapted in ways that

support cumulative cultural evolution.

22

5. CONCLUSIONS AND FUTURE DIRECTIONS

Cultural inheritance is what "makes us odd"(5); it plays a major role in making human minds and

lives radically different from those of other animals. This article has raised the possibility that

cultural learning is itself culturally inherited – rather than being genetic adaptations, the

psychological processes that make cultural inheritance possible are learned in the course of

ontogeny through social interaction. It has begun to investigate this possibility by looking at three

types of cultural learning: reading, social learning and imitation. In the case of social learning,

current evidence suggests that the core mechanisms of learning have not been adapted – either

genetically or culturally – to promote cultural inheritance. However, there are signs that input

mechanisms can be biased towards social sources, and, in humans, that these adaptive biases can be

driven by social interaction. Thus, the input mechanisms, or psychological 'mills', that modulate

social learning have characteristics that are culturally inherited – e.g. offspring inherit from their

cultural parents a tendency to focus on the eyes, or on the eyes and mouth, when viewing facial

expressions of emotion (31) – and these mill characteristics influence the 'grist' that is culturally

inherited through social learning – e.g. beliefs about what kinds of foods are and are not disgusting.

In the cases of reading and imitation, the evidence indicates that core cognitive mechanisms,

new modules, are constructed through social interaction. Learning to read reconfigures the

neurocognitive system to create several distinct routes for word recognition and reading aloud. It is

not only the grist of what we read – the ideas and values coded in text – but also these routes, these

psychological mills, which are passed down from one cultural generation to the next through literacy

training. Similarly, correlated experience of seeing and doing the same actions (e.g. while engaging

in synchronous action, and being imitated) makes imitation possible by establishing a vast repertoire

of matching vertical associations, many of which are embodied in the mirror neuron system.

Matching vertical associations are the culturally inherited mills which enable, and are enabled by,

the cultural inheritance by imitation of grist consisting of specific techniques, practices and rituals.

To find out more about the origins of cultural learning we need experiments explicitly

designed to test genetic adaptation against cultural adaptation hypotheses. This is, of course, very

difficult to do. The hypotheses relate to evolutionary history, but the minds available for

experimental analysis are of adults, children and nonhuman animals alive today. However, training

studies, which examine the effects of novel experience on cultural learning, and cross-cultural

studies, comparing cultural learning in groups that have received different sociocultural experience

throughout life, can tell us a lot about the poverty, or wealth, of the stimulus. To the extent that the

neurocognitive mechanisms of cultural learning have features they could not have acquired in the

course of development, genetic adaptation is implicated. To the extent that they have features that

could be acquired in the course of development, and that co-vary flexibly with sociocultural

experience, cultural adaptation is implicated. Distinguishing genetic from cultural origins is a thorny

methodological problem, but it is also one in which the burden of proof is equally distributed. As the

example of reading illustrates most clearly, we know that cultural learning can be culturally

inherited. Therefore, we cannot assume by default that any given type or feature of cultural

learning is a genetic adaptation.

It is also important to extend the enquiry from reading, social learning and imitation to other

types of cultural learning - including social motivation, theory of mind, teaching/pedagogy, and norm

representation – and, if further research confirms that cultural learning is to a significant extent

culturally inherited, to address the broader implications of this discovery. Perhaps the most far-

reaching of these concerns the extent to which cultural evolution is constrained by biological

evolution. If it is not just the grist but also the mills that are culturally inherited, cultural evolution

may be on a remarkably long 'genetic leash' (65).

Good, hard questions hover over any discussion of the evolution of human cognition. What

made the evolution of human minds 'take off'? How exactly do our minds differ from those of other

animals? These are important questions but we must be careful not to turn them into a party game

where the prizes go to simple, spectacular answers (66). It would be convenient if we could identify

24

a 'big bang' of human cognitive evolution, or a small number of distinctively human, genetically

evolved cognitive modules. However, as many of the articles in this theme issue make clear, the

true story is more likely to be one in which multiple sources of selection pressure resulted in gradual

gene-culture co-evolution of a distinctive set of cognitive processes. The view advanced in this

article – that mechanisms of cultural learning are themselves culturally inherited – is compatible

with the idea that human cognitive processes are distinctive in their plasticity and domain-generality

(67, 68); in the degree to which they have released us from genetically determined modularity of

mind. More specifically, it suggests that much of this has been achieved by increases in the range

and power of associative learning, and the gene-culture co-evolution of sequence processing

mechanisms; mechanisms, now involved in processing vocal language and imitation learning, that

began to evolve in the context of tool making and gestural communication (69). It also implies that a

good deal of the heavy lifting in the evolution of human cognition has been done by genetic and

cultural adaptation of input mechanisms rather than core cognitive mechanisms; by perceptual

specialisations, attentional biases, inhibitory processes, and motivational changes of the kind that

yield social tolerance (52). It is not one big thing, but many small things, that 'make us odd'.

26

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28

Page 29 of 34

Submitted to Phil. Trans. R. Soc. B - Issue

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Figure Legends

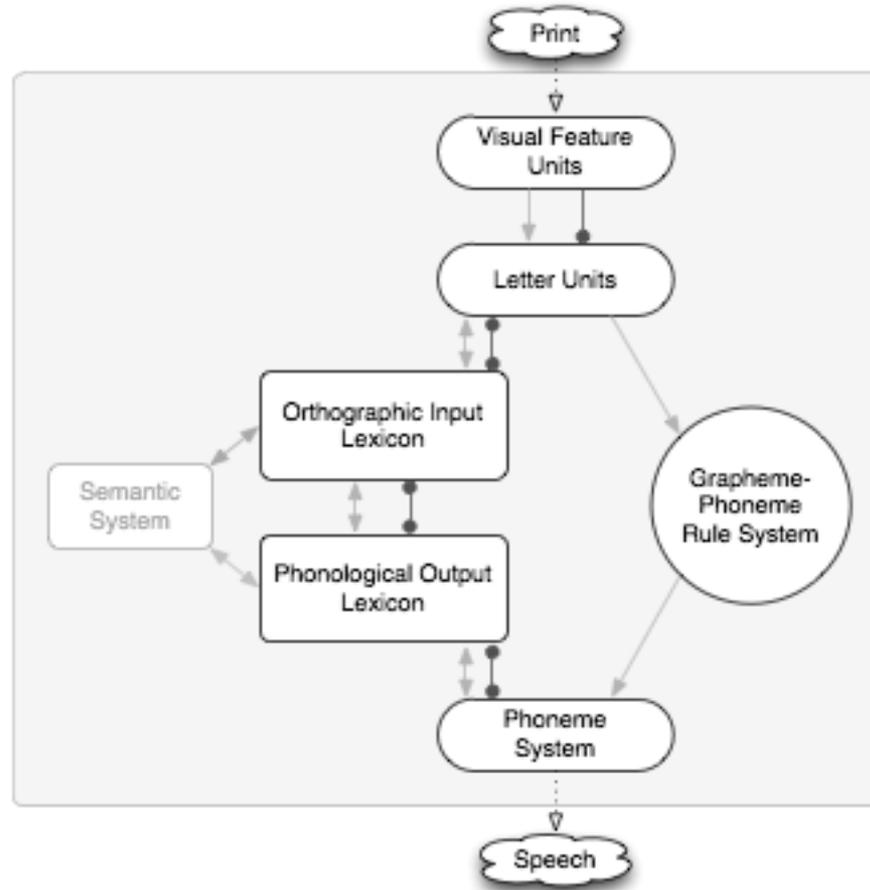Figure 1. The Dual Route Cascaded (DRC) model of visual word recognition and reading aloud.

Figure 2. The Associative Sequence Learning (ASL) model of imitation.

Figure 3. Summary of research on imitation in neonates and young infants. The number of published experiments reporting positive results (dark bars) and negative results (lighter bars) for each of the eight gestures tested.

30

Page 31 of 34

Submitted to Phil. Trans. R. Soc. B - Issue

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Short title: Cultural learning

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HORIZONTAL

Sensory$_1$

Sensory$_2$

Sensory$_n$

VERTICAL

Motor$_1$

Motor$_2$

Motor$_n$