

IMITATION AND CULTURE: LONGEVITY, FECUNDITY AND FIDELITY IN SOCIAL TRANSMISSION

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ABSTRACT This paper examines the significance of imitation in nonhuman animals with respect to culture. It is argued that imitation (learning about behaviour through conspecific observation) is no more likely than social learning (learning about the environment through conspecific observation) to mediate cultural transmission of information. Both social learning and imitation allow information about behaviour to be transmitted. The process of information acquisition is less selective in the case of imitation, and therefore imitation-transmitted units have greater longevity. However, because they are not unselectively retained, units acquired through imitation have no more fidelity or fecundity than those acquired through social learning, and are therefore no more likely to afford stability of behavioural traditions or cultural accumulation of information. This analysis implies that culture is a uniquely human phenomenon and that cultural transmission of information occurs primarily through instruction.

SOCIAL LEARNING VS IMITATION

Imitation is commonly regarded as a special, or even hallowed, form of social learning. It has been claimed to have dual significance; to be unique both in its cognitive complexity (e.g. Morgan, 1900; Galef, 1988; Lefebvre and Palameta, 1988; Whiten and Ham, 1992) and in its potential to support culture (e.g. Dawkins, 1976; Boyd and Richerson, 1985; Whiten, 1989; Galef, 1992; Laland et al, 1992). I will argue that while imitation is indicative of some interesting and mysterious cognitive processing in animals, it does not mediate cultural transmission of information. However, first I should clarify what I mean by 'imitation', a term which has been transmitted among scientists with remarkably little fidelity.

Environment and Behaviour

Imitation may be distinguished from other forms of social learning according to what is learned through conspecific observation. In non-imitative social learning, observers learn about stimuli, objects or events in the environment - either to distinguish them from other classes of stimuli or that they have a positive or negative value by virtue of their relationships with other objects and events. For example, rhesus monkeys avoid snakes (i.e. snakes

acquire a negative value for them) after they have observed a conspecific behaving fearfully towards snakes (Cook et al., 1985). When red-winged blackbirds have observed a healthy conspecific feeding from a distinctive container, they consume more from that cup; and when they have observed a conspecific feeding from a container and then avoiding it and showing signs of illness, they avoid the cup themselves (Mason and Reidinger, 1981; 1982). Distinctive diets become attractive to rats when their odour has been detected on the breath of a conspecific (Galef and Stein, 1985). Octopuses selectively attack objects that have been observed under attack by a conspecific (Fiorito and Scotto, 1992). Rhesus monkeys that have observed a conspecific choosing one of two objects to obtain food, will select the same object if the demonstrator's choice was rewarded, and the other object if that choice was not rewarded (Darby and Riopelle, 1959; Riopelle, 1960).

In imitative social learning, on the other hand, the observers learn through conspecific observation about responses, actions, or patterns of behaviour. Observers may acquire the plan, or "impulse" (Thorndike, 1898) for a novel behaviour pattern, and/or learn that a certain behaviour pattern has a particular consequence or outcome (Tomasello et al., 1987). The former effect is sometimes called "copying" (Galef, 1988) and is common among passerine birds that acquire species- or locale-specific song from conspecifics (e.g. Petrinovich, 1988). The possibility that an observer may learn about an action-outcome relationship without acquiring a novel behaviour pattern has not been considered explicitly, but hypothetical cases in which the observer both acquires a novel behaviour and learns about its outcome have been described as instances of "observational learning" (Hall, 1963), "reflective imitation" (Morgan, 1900) and "true imitation" (Thorpe, 1963). In this paper, I shall refer to non-imitative social learning (about environmental events or stimuli) as 'social learning', and to imitative social learning (about behaviour or responses) as 'imitation'.

Evidence of Non-vocal Imitation in Animals

There are, to my knowledge, only two published studies providing convincing evidence of non-vocal imitation in animals. Both of these studies have compared the behaviour of animals that have observed demonstrators interacting with a single object or manipulandum in different ways. Galef et al. (1986; following Dawson and Foss, 1965) allowed budgerigars to observe a conspecific using either its beak or its feet to remove a flat cover from the top of a cup containing seed. When the observers were given access to a cup and cover apparatus immediately after each demonstration, they showed a significant tendency to use the same appendage to remove the cover as had their demonstrator.

In the second study (Heyes and Dawson, 1990), rats observed a trained conspecific pushing a joystick that was hanging vertically from the ceiling of one compartment of a dual-compartment operant chamber (Figure 1). One

group observed demonstrators pushing to the 'left' (directly towards the viewer of Figure 1), and the other observed demonstrators pushing to the 'right' (directly away from the viewer of Figure 1) for food reward. When the demonstrator had made 50 responses, the observer was transferred to the test compartment and given access to the joystick for the first time. In the ensuing test session, the observers were rewarded by the delivery of a food pellet both for pushing left and for pushing right. However, those animals that had observed left pushing made a significantly greater proportion of their responses to the left than did those animals that had observed right pushing. On average, the observers of left pushing made 86% of their pushes to the left, and observers of right pushing made 29% of their pushes to the left.

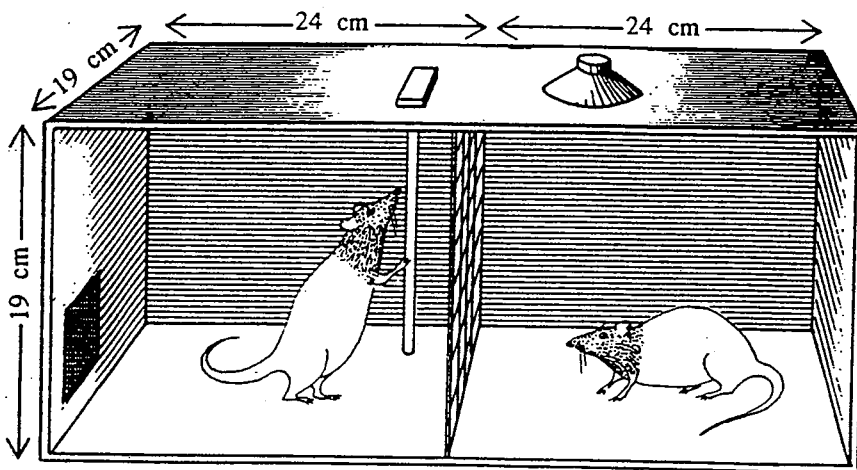


Figure 1. Diagram of apparatus used by Heyes and Dawson (1990). Reprinted with the permission of the Experimental Psychology Society from *Quarterly Journal of Experimental Psychology*, 42B, 59-71.

In order to provide a more rigorous test, in a subsequent experiment the joystick was moved between observation and testing (Heyes et al., 1992). While the subjects were observing their demonstrators' performance, the joystick was in the position indicated in Figure 1. Before the observers were tested, the joystick was moved so that it hung in the middle of the front wall of the same compartment. Consequently, while a 'right' push by a demonstrator resulted in the tip of the joystick moving towards the back of the box, a 'right' push by an observer resulted in the tip moving towards the partition; towards the corner into which it moved when a demonstrator made a 'left' push. Despite this transposition, observers of right pushing made a greater proportion of their responses to the right than did observers of left pushing. That is, each observer

tended to push the joystick in the same direction, relative to its own body, as had its demonstrator. Rats do not show any systematic directional preference when they have observed, in the absence of a conspecific demonstrator, the joystick moving automatically to the left or to the right (Heyes et al., 1992).

These studies indicate that budgerigars and laboratory rats are capable of imitation; of response learning through observation. The majority of other attempts to demonstrate the phenomenon have used field or laboratory methods that lack the potential to distinguish imitation from other forms of social learning (Galef, 1988 and 1992; Hogan, 1988; Heyes and Dawson, 1990; Visalberghi and Frigaszy, 1990). Consequently, it would be wrong to assume without further, methodologically sound research that imitation is only found in budgerigars and rats, or even that it is rare within the animal kingdom (contra Whiten and Ham, 1992). Hypotheses about the ecological conditions favouring the evolution of imitation (e.g. Lefebvre and Palameta, 1988; Laland et al., 1992) also appear to be premature.

Imitation and Cognition

The imitation of certain kinds of actions by animals has potentially far-reaching implications for our understanding of animal cognition. The actions in question are those that yield very different sensory inputs to an animal, O, when O performs them, and when O observes them being performed by another animal D. This is the case for facial expressions and many whole body movements (including cup cover removal by budgerigars and joystick pushing by rats), but not for vocal behaviours. To take a human example, consider the case of the whole body movement curtsyng. If I look down when I curtsy, I see something very different from what I see when I look across at somebody else curtsyng. If animals can imitate movements like this without being rewarded for successive approximations to the modelled movement, then it is something of a mystery. Humans might know that they are performing the same movement as a result of exposure to mirrors, but how might an animal, that has not seen reflections, map visual input from a model onto disparate visual and/or kinesthetic feedback from their own actions? In attempting to answer this question, we may find that animals can manipulate and transform information in ways that have hitherto been assumed to be beyond their capabilities (Heyes, 1992).

In this section I have distinguished imitation (learning about behaviour through conspecific observation) from social learning (learning about the environment through conspecific observation) in a way that is conventional among psychologists and ethologists, presented evidence of non-vocal imitation in animals, and affirmed that such evidence has considerable significance with respect to animal cognition. In the next section I shall consider whether research on imitation in animals is also likely to make a special contribution to our understanding of culture.

IMITATION AND CULTURE

Some investigators assume that both social learning and imitation can produce "traditions" (Morgan, 1900; Mainardi, 1980; Roper, 1980) or mediate "cultural transmission" (Bonner, 1980; Sherry and Galef, 1984), but many argue or assume that there is a special relationship between imitation and culture (e.g. Dawkins, 1976 and 1982; Mundinger, 1980; Hull, 1982; Boyd and Richerson, 1985; Rogers, 1988; Whiten, 1989; Dennett, 1990; Galef, 1992). The latter view is reflected in the use of terms such as "protoculture", "subculture", or "preculture" to describe behaviour thought to have been acquired through imitation (Galef, 1988).

Many of those who argue that imitation has a special significance with respect to culture have a distinctive, evolutionary conception of culture. They do not regard a culture merely as a set of behaviours or ideas acquired through social interaction and consequently shared by the members of a social group. For them a culture is a population of cultural variants, or "memes" (from the Greek 'mimeme' - an imitable entity, Dawkins, 1976), that has evolved through variation and selective retention; i.e. through a process analogous with, or logically identical to, that which gives rise to biological adaptations and ultimately to species (e.g. Dawkins, 1976 and 1982; Plotkin and Odling-Smee, 1981; Hull, 1982; Boyd and Richerson, 1985; Laland et al., 1992). Cultural evolution of this kind can occur only if there is a process, analogous to biological reproduction, enabling cultural variants to move from one individual to another within a social group; it has been claimed that imitation can, and social learning cannot, fulfil this function (Dawkins, 1976; Hull, 1982; Boyd and Richerson, 1985; Laland et al., 1991). Three arguments have been advanced in support of this evolutionary conception of the role of imitation in culture. I shall evaluate each in turn, suggesting that it is not persuasive.

Information and Behaviour

First, it has been suggested that imitation does, and social learning does not, allow cultural transmission because imitation involves information acquisition, while social learning merely consists of a change in behaviour (Boyd and Richerson, 1985). The information-behaviour distinction is important because if cultural evolution is truly analogous to Darwinian, biological evolution (or, more precisely, if cultural evolution is truly Darwinian evolution), then it must be possible for individuals to acquire ideas or information (the analogue of genes), rather than behaviour (the analogue of phenotypic characteristics), through social interaction (Hull, 1982; Boyd and Richerson, 1985).

The claim that imitation and social learning involve information and behaviour acquisition, respectively, is understandable but not justified. It

appears to have arisen from a misinterpretation of the view, originally advanced by Galef (1976), that imitation is unique in requiring a 'cognitive', rather than a 'behavioural' explanation. It is true that imitation is the only social learning phenomenon that has been acknowledged by investigators to be resistant to explanations that do not refer to unobservable psychological processes. However, this historical phenomenon does not indicate that imitation is alone in involving such processes; in being 'cognitive', and therefore, by implication, involving the acquisition of information (Heyes and Plotkin, 1989). This is an empirical issue, and one which has been largely resolved in favour of the view that both social learning and imitation involve information acquisition.

The relevant experiments have shown that perceptual learning and classical conditioning phenomena are mediated by cognitive representations (Dickinson, 1987). For example, rats which have been exposed to repeated pairings of a tone and food, will acquire an aversion to that food when they are poisoned after hearing the tone (Holland, 1981). This suggests that, as a result of the tone-food pairings, the tone had acquired the capacity to activate a cognitive representation of the food, and that it was the experience of sickness in association with this representation which led the rats subsequently to avoid consuming the food. If learning under these conditions is mediated by cognitive representations, then there is little reason to doubt that, not only imitation, but also social learning, is typically 'cognitive'. Many examples of social learning are equivalent, at a descriptive level, to classical conditioning. They involve a change in behaviour towards an object or event as a result of exposure to a contingency between that stimulus and some other stimulus. In the case of social learning, conspecific behaviour either brings about stimulus exposure, and/or constitutes the 'other stimulus', but there is no reason to suppose that this difference, in the conditions of learning, signifies a difference in the process of learning.

Acquisition and Transmission

The second argument favouring imitation as a process of evolutionary, cultural transmission runs roughly as follows. Both social learning and imitation involve information acquisition, but only imitation effects information transmission. The latter occurs when a faithful copy of some information present in one animal, appears in a second animal as a result of its interaction with the first. Information transmission is necessary for cultural evolution because it is an energetically cheap, and direct way of acquiring information, and in its absence the accumulation of information and stability of traditions, which is characteristic of human culture would not be possible (Boyd and Richerson, 1985; Galef, 1992; Laland et al., 1992). Contrary to this view, there is reason to believe that 1) social learning can effect information transmission, and 2) imitation is not cheap and direct in a way that could support cultural accumulation or the stability of traditions.

The primary evidence that social learning can effect information transmission comes from nearly 100 years of research which failed to provide evidence of imitation in non-human animals (Roper, 1980; Galef, 1988). Each time behavioural data have been put forward as evidence of imitation, it has subsequently been discovered that those data can be explained in terms of social learning: that, after observation, the observers may have behaved in the same way as the demonstrators because they had learned about their environment, rather than behaviour, while observing. This indicates that social learning - learning about the environment, rather than behaviour, through conspecific observation - has considerable potential to mediate both behaviour and information transmission. If this were not the case, social learning and imitation would have proved much easier to distinguish empirically.

As an illustration of information transmission through social learning, consider the case of some pigeons that observed conspecifics pecking a red spot on a sheet of paper covering a box of seed, piercing the paper in the region of the spot, and consuming the food inside (Palameta and Lefebvre, 1985). These pigeons were subsequently more likely to pierce similar covers than birds which had not observed the piercing behaviour, and this effect is likely to have been due to social learning rather than imitation (Heyes and Dawson, 1990). That is, the demonstrators' behaviour probably drew the observers' attention to the red spot, and ensured that the sight of the red spot was followed by the sight of food on several occasions. As a result, the observers learned through observation alone that the red spot was associated with food, and on the basis of this information subsequently approached and pecked the spot causing the paper to break. This experience, which they would not have had if they had not observed the demonstrators, allowed observer pigeons to learn that pecking the seed-box cover had a certain outcome, i.e. to acquire the information that had been generating the demonstrator's behaviour.

Although social learning rather than imitation was involved, this is an example of behaviour transmission mediated by information transmission. It is behaviour transmission in that the piercing technique, which was once executed only by demonstrator birds, was later also executed by observer birds because they had observed the demonstrators. This behaviour transmission was mediated by information transmission in that, as a result of observing demonstrators, observers acquired information that had been generating demonstrators' behaviour, viz. that a certain behaviour had a certain outcome. The observers did not acquire this information by observation alone; they also had to act on the world themselves. The necessity of observer action is what makes this an example of social learning, rather than of imitation. However, the insufficiency of the observation experience does not detract from the fact that this is an example of information transmission. The important point is that conspecific observation played a significant causal role in acquisition by observers of information that had generated demonstrators' observed behaviour.

Having shown that social learning, like imitation, can mediate information transmission, I shall now move on to the question of whether imitation constitutes a mode of transmission that is, by virtue of being cheap and direct, more likely than social learning to result in cultural accumulation and stable traditions. This has been assumed, not only by investigators of cultural evolution, but also by those with a more general interest in the evolution of culture (e.g. Galef, 1992; Whiten and Ham, 1992).

It is currently impossible, in practice, to evaluate the suggestion that imitation is energetically cheaper than social learning. By definition, imitation allows information about a behaviour-outcome relationship, or the plan of a novel behaviour, to be acquired through conspecific observation alone, while social learning requires an animal both to observe a conspecific and to interact directly with the environment in order to learn about behaviour. Consequently, when it comes to learning about behaviour, imitation represents a potential economy of time, effort and risk, but we do not know whether it would beat social learning in a more global, and therefore realistic, cost-benefit analysis (Johnston, 1981). The energetic costs of, for example, developing and maintaining the cognitive 'plant' necessary for imitation, and the risks associated with close attention to the behaviour of a conspecific, are currently inestimable.

The claim that imitation is more direct than social learning is more complex, but also ultimately more empirically tractable than the suggestion that imitation is cheap. It is more complex because imitation is more direct than social learning, but not in a way that could be expected to promote cultural accumulation and stable traditions. Imitation is more direct in that it allows an animal to acquire information about a behaviour without the validity of that information being checked in the process. In order for information about behaviour to be acquired through social learning, the animal must act on what it has learned about the environment through observation, and as a result of that action it may end up acquiring information that differs from that which was driving the demonstrator's behaviour. For example, if the pigeons in our earlier example had learned by observation that a certain behavioural technique could be used to gain access to the seed (imitation), they would be expected initially to apply that technique even if an alternative would be equally effective. On the other hand, if the birds had learned by observation about the red spot-food relationship (social learning), some of them could be expected, as a result of their interactions with the seed box, to employ an equally effective alternative technique, indicating that they had ultimately learned a different behaviour-outcome relationship than the demonstrator. Thus, behaviours that are equally effective or less effective than alternatives are more likely to be selected out of a population in the process of social learning than in the process of imitation.

The fact that imitation is a relatively direct means of acquiring information about behaviour should not, however, lead us to think that it can

support cultural accumulation and the stability of traditions. Imitation could be expected to have these effects only if information acquired through imitation were directly, or preferentially, retained and utilised; that is, if it were more likely than information acquired through other forms of learning to be retained when it gives rise to behaviour that is punished, rewarded less than alternative behaviour, or rewarded only as often as alternative behaviour. The available evidence, from both humans and other animals, suggests that this is not the case. For example, children who behave aggressively towards a doll as result of observing that behaviour in an adult, will cease to do so if their aggressive behaviour is punished (Bandura and Walters, 1963). When rats are rewarded for pushing a joystick to the left, and not for pushing it to the right, those that have observed a conspecific pushing to the right and being rewarded initially push to the right more than those that have observed rewarded left-pushing. However, after the observers have made 10 responses, this tendency disappears, and both groups push predominantly to the left (Heyes and Ray, unpub). Budgerigars that have observed a conspecific removing a cup cover with its beak or with its feet, show a tendency to use the same appendage as their demonstrator to remove the cover only on the first two trials after observation. Subsequently, those that observe beak-use before each trial are no more likely than those that observe feet-use before each trial to remove the cover using their beak (Galef et al, 1986).

These examples suggest that behaviour acquired through imitation is not preferentially retained, and consequently make it unlikely that imitation is better able than social learning to support stable, behavioural traditions. It could be argued that imitation may still play a unique role in cultural accumulation (Galef, 1992) because what is 'accumulated' is knowledge or information, and the information, if not the behaviour, acquired through imitation may be preferentially retained. I know of no evidence bearing on this possibility; for example, studies showing that behaviour initially acquired through imitation is more readily re-learned than behaviour acquired through social learning, or, in the human case, that people give a more accurate verbal report of information acquired through imitation, when they do not use it to guide their non-verbal behaviour. I see no a priori reason to anticipate such effects, and, even if they exist, I doubt that they would either allow cultural accumulation in animals, or significantly facilitate cultural accumulation in humans.

In animals, information transmission depends crucially on behaviour transmission. Items of acquired information can be transmitted only to the extent that they are used to guide behaviour by their holders, and consequently preferential retention of information acquired through imitation could not support cultural accumulation unless it were accompanied by preferential retention of behaviour. In humans, on the other hand, information transmission is to a large extent decoupled from behaviour transmission because language and artefacts allow information that is not in use to be passed on. Indeed, language

and artefacts provide such enormous potential for cultural accumulation that there is little reason to ascribe a significant role to imitation.

Before considering the final argument favouring a special role for imitation in culture transmission, it should be noted that birdsong imitation or "copying" (Galef, 1988) represents a somewhat different case than those mentioned above. Here the acquisition of information about behaviour (the "template" or "engram" for particular vocal patterns) does not depend on observation of the outcome of the behaviour for the demonstrator, and beyond a certain stage in ontogeny the information is retained in spite of exposure to alternative models (e.g. Petrinovitch, 1988). However, birdsong imitation phenomena do not support the general claim that imitation, rather than social learning, constitutes cultural transmission for two reasons. First, they show that imitation can contribute to stable traditions of vocal behaviour, under conditions of fairly tight genetic constraint, in the absence of differential reward, and when alternative behaviours are neutral with respect to adaptation (Lynch et al., 1989), and this set of conditions is not typical of traditions. Second, birdsong imitation phenomena provide no evidence of cultural accumulation of information.

Simple and Complex

It has been suggested that imitation is more important with respect to culture than social learning because it is only through imitation that large amounts of complex information can be transmitted (Lefebvre and Palameta, 1988; Laland et al, 1992). The view that imitation provides for the transmission of more complex information appears to rest on two assumptions: 1) that information about behaviour or responses (imitation) is more complex than information about stimuli or the environment (social learning), and 2) that the only information that is transmitted is that which is acquired directly through conspecific observation. The latter assumption was challenged in the previous section, and the former appears somewhat arbitrary. When 'complex' is taken to mean 'more difficult for researchers to understand', imitation is certainly mediated by more complex cognitive processes than social learning, and may be said to involve the acquisition, during observation, of more complex information. However, this is not a dimension of complexity that is directly relevant to cultural evolution, or the evolution of culture. In order to show that imitation has a special relationship with culture by virtue of the complexity of the information it transmits, it would be necessary to specify what is meant by 'complex' and to say why imitation might lie higher on the relevant scale than social learning.

The suggestion that imitation effects the transmission of a larger amount of information than social learning presents an interesting empirical question, but one that has not yet been addressed. I do not know of any studies directly comparing the amount of information typically transmitted via these two routes,

but there is evidence suggesting that 'small is beautiful' with respect to imitation-mediated transmission. In a study of the cultural evolution of chaffinch song, Lynch et al. (1989) found an inverse relationship between the length of syllable sequences and the probability of their imitation-mediated cultural transmission.

Longevity, Fecundity and Fidelity

The foregoing discussion of the relationship between imitation and culture can be summarised and extended with reference to the suggestion that units can become the basis for natural selection and consequently for evolution only if they have "Longevity, Fecundity, Fidelity" (Dawkins, 1978 and 1982). That is, if they produce additional units (fecundity), that have basically the same structure as the originals (fidelity), because they were produced by those units (longevity), and if the units are in a position to produce in this way "an indefinitely long line" (Dawkins, 1982: p.83) of descendant units. According to this analysis, imitation would be more important than social learning with respect to cultural evolution if it allowed cultural units, pieces of information or 'ideas', 1) to produce additional units in a greater number of other animals (fecundity), 2) to produce units more like themselves in other animals (fidelity), and/or 3) to produce units in other animals via a more direct causal sequence (longevity).

When imitation is distinguished from social learning according to what is learned during conspecific observation, there is no reason to suppose that it is associated with a significantly greater sum of longevity, fecundity and fidelity. Units of information about the environment are, by definition, transmitted only by social learning, and therefore the question of whether imitation would afford such units greater longevity, fecundity and fidelity does not arise. Imitation apparently allows units of information about behaviour to be transmitted - to produce other, similar units in other animals - via a more direct causal sequence than social learning. Imitation does not require the recipient animal to act on the world in order for transmission to be effected. Consequently, imitation may give units of information about behaviour greater longevity, but this is not important unless it thereby ensures or enhances their fidelity or fecundity. Imitation cannot be expected to produce a significant enhancement of fidelity because current evidence suggests that imitated information about behaviour is no more likely to be retained than socially learned information about behaviour. Therefore, while imitation may be associated with greater short-term fidelity of transmission, it cannot be expected to enhance fidelity in the long term; across a sequence of transmission episodes.

To illustrate this point, imagine that one could examine directly the information possessed by a demonstrator and an observer just after observation, and before the observer has had an opportunity to act on what it had learned by observation. If the observer had engaged in imitative learning during

observation, then one would, by definition, find that a unit of information about behaviour had been more faithfully transmitted from the demonstrator to the observer, than if the observer had engaged in social learning during observation. An imitator would have the same behaviour plan as that which allowed the demonstrator to execute his behaviour, or, like the demonstrator, would have the information that 'behaviour X leads to outcome Y.' A social learner, on the other hand, would have either a propensity to approach a certain part of its environment, or information about a relationship between two stimuli. The information about behaviour, possessed by the demonstrator, would not at that moment have been faithfully transmitted between the two animals. However, as soon as the observer uses the information that it has acquired, as soon as it converts that information into behaviour, this difference is liable to disappear.

If the observer's and demonstrator's environments are the same, and if there are relatively few alternative behaviours having the same consequences in that environment, a social learner could quickly come into possession of the information about behaviour that was driving the demonstrator's action. On the other hand, if the observer's and demonstrator's environments are different, or if there are relatively many alternative behaviours having the same consequences in their common environment, the information about behaviour acquired by an imitator could quickly be lost, modified or replaced. Such changes in the information acquired through imitation would prevent re-transmission, blocking long-term fidelity, and not in a way that constitutes the cultural equivalent of natural selection. The information would be selected out of the population of cultural units through the effects of the behaviour that it generates on the inanimate or acultural environment. It would not be selected out 'socially', through the agency of members of the social group or other "vehicles" (Dawkins, 1982) of culturally transmitted information. Thus, the long-term fidelity of a unit of information about behaviour, the fidelity that matters with respect to the possibility of cultural evolution, depends on the range of behavioural alternatives and the environment in which the information is used, not on whether the information was acquired through social learning or imitation. Similarly, the fecundity of units of information about behaviour is unlikely to depend on whether they are transmitted through social learning or imitation. A unit acquired through imitation would tend to be transmitted to a greater number of other animals than the same unit acquired through social learning, only if it is, by virtue of having been imitated in the first place, preferentially used by the demonstrator to guide its behaviour, or preferentially adopted by potential observers. That is, only if imitated information is more likely to be available for transmission, or, while equally likely to be available, is in some sense more acceptable to observers. The latter possibility need not be considered seriously since it is not clear how an observer could know, or why it would care, whether the information generating a conspecific's behaviour had been acquired through social learning or imitation. Regarding availability, since

there is no evidence that imitated information is more likely to be retained than socially learned information, there is no reason to suppose that imitated information is available more often, or for longer. Imitated information may become available sooner after conspecific observation, but this possibility represents an unresolved empirical question. In principle, an imitator is in a position to re-transmit information about behaviour with its first action after conspecific observation, while a social learner must first act on the environment to convert into information about behaviour the information about stimuli that it acquired during observation. However, imitation may not, in practice, fulfil its potential for speedy re-transmission. Depending, perhaps, on the intricacy and novelty of the behaviour in question, the imitator may have to develop the motor skill through practice. Since a social learner might be developing the skill at the same time as converting information about stimuli into information about behaviour, it may have the information available for re-transmission just as soon.

The foregoing review of reasoning and evidence suggests that imitation is no more likely than social learning to support culture. Both social learning and imitation allow information about behaviour to be transmitted. The process of information acquisition is more direct in the case of imitation, and therefore imitation-transmitted units have greater longevity. However, because they are not directly or preferentially retained, units acquired through imitation have no more fidelity or fecundity than those acquired through social learning, and are therefore no more likely to afford stability of behavioural traditions or cultural accumulation of information.

CONCLUSION: PEOPLE AND ANIMALS

The relevant evidence is scant, and the reasoning necessarily complex, so the conclusion that imitation is no more likely to support culture than social learning may have to be revised in the light of further research. However, let us suppose that it is correct and consider, briefly, its implications.

The first, and most obvious implication is that research on imitation in non-human animals has no bearing on "the question of animal culture" (Galef, 1992). Establishing whether the members of any given species are capable of imitation in addition to social learning may ultimately tell us a great deal about the sophistication of their cognitive functioning, but it will not tell us whether they are capable of taking part in cultural exchange. A second, closely related implication is that research on imitation in animals is no more likely than research on social learning to indicate the evolutionary precursors, or phylogenetic origins, of human culture (Boyd and Richerson, 1985).

These implications are modest in that they leave open the possibility that both imitation and social learning can support culture. This is implausible given that the information acquired through both routes is not preferentially retained;

that it is subject to continual revision resulting from the learner's interactions with its inanimate environment. If we assume instead that neither social learning nor imitation can support culture, then a more radical implication emerges: that culture is not to be found among nonhuman animals. This is implied because nonhuman animals apparently lack any other means of supporting cultural accumulation of information or, more specifically, cultural evolution. People instruct one another, either linguistically, or by modifying their non-verbal behaviour such that observers are more likely to acquire or retain certain information. We also produce durable artefacts - monuments, scrolls, and books - which, through their linguistic inscriptions, transmit information with high fidelity to individuals living in very different environments. It is these linguistic and paedagogic capabilities that are, in my view, likely to be central with respect to the human capacity for culture, but there is no evidence of either true language or tuition in nonhuman animals (Ewer, 1969; Hinde, 1971; Premack, 1991; Galef, 1992).

If imitation plays an important role in human language acquisition, and if language is a pre-requisite for culture, then in humans imitation has a special relationship with culture. However, if my analysis is correct, imitation does not itself constitute a process of cultural transmission in either people or animals.

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