

Imitation, culture and cognition

C. M. HEYES

Department of Psychology, University College London, Gower Street, London WC1E 6BT, U.K.

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Abstract. This paper examines the significance of imitation in non-human animals with respect to the phylogenetic origins of culture and cognitive complexity. It is argued that both imitation (learning about behaviour through conspecific observation) and social learning (learning about the environment through conspecific observation) can mediate social transmission of information, and that neither is likely to play an important role in supporting behavioural traditions or culture. Current evidence suggests that imitation is unlikely to do this because it does not insulate information from modification through individual learning in the retention period between acquisition and re-transmission. Although insignificant in relation to culture, imitation apparently involves complex and little-understood cognitive operations. It is unique in requiring animals spontaneously to equate extrinsic visual input with proprioceptive and/or kinaesthetic feedback from their own actions, but not in requiring or implicating self-consciousness, representation, metarepresentation or a capacity for goal-directed action.

Research on imitation in non-human animals has addressed three principal questions. (1) How should imitation be defined and distinguished from other forms of social learning (e.g. Thorndike 1898; Morgan 1900; Thorpe 1956; Galef 1976, 1988; Zabka & Tembrock 1986; Whiten & Ham 1992)? (2) Are animals capable of imitation (e.g. Thorndike 1898; Watson 1908; Haggarty 1909; Humphrey 1921; Warden & Jackson 1935; Miller & Dollard 1941; Hayes & Hayes 1952; Dawson & Foss 1965; Galef et al. 1986; Tomasello et al. 1987; Heyes & Dawson 1990; Visalberghi & Frigaszy 1990a)? (3) What is, or would be, the significance of imitation in animals? In this paper I examine the third question, with a view to encouraging investigation of a fourth, neglected, issue: what are the psychological processes mediating imitation in animals? Imitation has been claimed to have dual significance: to be unique among varieties of social learning both in its potential to support culture (e.g. Washburn 1908; Piaget 1962; Huxley 1963; Bruner 1972, 1983; Lorenz 1974; Dawkins 1976; Boyd & Richerson 1985; Bandura 1986; Lefebvre & Palameta 1988; Whiten 1989; Galef 1992; Tomasello et al., in press), and in its cognitive complexity (e.g. Thorndike 1898; Morgan 1900; Piaget 1962; Galef 1988; Whiten & Ham 1992). I argue against the first of these claims, and in favour of the second: that imitation involves complex and little understood

psychological processes, but that it is unlikely to provide a basis for cultural exchange.

Before discussing the potential significance of imitation, it is necessary to provide reasonable, but not complete, answers to the other two questions. Consequently, in the first section, I distinguish imitation from other forms of social learning, and provide evidence that at least some non-human animals are capable of imitation.

DEFINITIONS AND EVIDENCE

At various times in the last century, and for various reasons, psychologists and biologists have distinguished a bewildering array of imitative phenomena, ways in which the behaviour of one animal can influence that of another. These phenomena include: instinctive imitation (Morgan 1900); stimulus enhancement (Spence 1937); matched dependent behaviour (Miller & Dollard 1941); mimesis (Armstrong 1951); local enhancement (Thorpe 1956); vicarious instigation (Berger 1962); observational learning (Hall 1963); true imitation (Thorpe 1956); social facilitation (Zajonc 1965); and observational conditioning (Cook et al. 1985). Taxonomies that include all, or a large proportion, of these distinctions (e.g. Galef 1988; Whiten & Ham 1992) are of considerable historical

interest, but they are poor guides for scientific research. Rather than distinguishing types of imitative behaviour within a single, currently acceptable, theoretical framework, they commonly differentiate varieties of scientific thinking (e.g. classical ethology, cognitive ethology, Hullian behaviourism, operant psychology, Pavlovian associationism), and ultimately reveal more about the investigation of imitative phenomena than about their animal subjects (Heyes & Plotkin 1984, 1989). Consequently, the present analysis is based on a simple distinction between 'imitation' and 'social learning' that elides the intricacies of most taxonomies while defining imitation in a conventional, if not consensual, way. Imitation differs from other forms of social learning in terms of what is learned as a direct result of observation or interaction with another animal (typically a conspecific) or its products (e.g. scent marks, burrows, exploited and discarded food items, video-recordings of its behaviour). 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 to attach to them a positive or negative value by virtue of their relationships with other objects and events. For example, rhesus monkeys, *Macaca mulatta*, 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, *Agelaius phoeniceus*, 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 & Reidinger 1981, 1982). Distinctive diets become attractive to rats, *Rattus norvegicus*, when their odour has been detected on the breath of a conspecific (Galef & Stein 1985). Octopuses, *Octopus vulgaris*, selectively attack objects they have observed under attack by a conspecific (Fiorito & Scotto 1992).

In imitative social learning, on the other hand, observers learn as a direct result of conspecific observation about responses, actions, or patterns of behaviour. Specifically, individuals acquire, as a result of observing a conspecific's behaviour, X, the capacity to execute a behaviour that is topographically similar to X, and, in some cases, the information that X has a certain consequence or outcome (Mackintosh 1983). When learning of an action-

outcome relationship by observation is not implicated, imitative social learning is sometimes called 'copying' (Galef 1988), and exemplified by those passerine birds that acquire species- or locale-specific song from conspecifics (e.g. Petrinovich 1988). Hypothetical cases in which the observer both acquires the capacity to execute a behaviour and learns about its outcome through observation have been described as instances of 'observational learning' (Hall 1963), 'reflective imitation' (Morgan 1900) and 'true imitation' (Thorpe 1956). 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'.

There is no doubt that parrots (*Chrysotis* spp.) and many passerine birds exhibit vocal imitation, but to my knowledge there are only two published studies providing convincing evidence of non-vocal imitation in animals. Both of these studies have used a 'pattern control' (Galef 1988; Heyes et al. 1992) or 'cross target' (Meltzoff 1988) procedure; they 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 & Foss 1965) allowed budgerigars, *Melopsittacus undulatus*, 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 & 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 (Fig. 1). One group observed demonstrators pushing to the 'left' (directly towards the viewer of Fig. 1), and the other observed demonstrators pushing to the 'right' (directly away from the viewer of Fig. 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

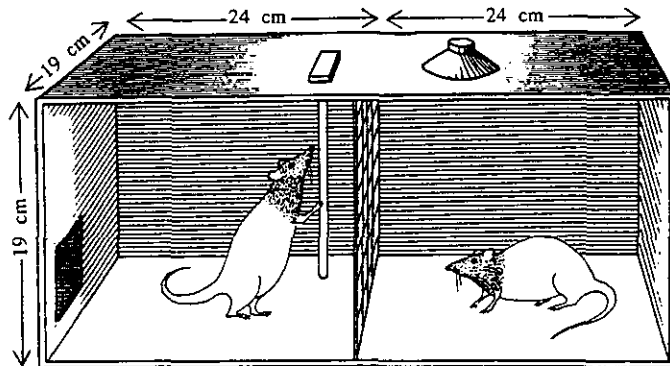


Figure 1. Diagram of the apparatus used by Heyes & Dawson (1990) in their bidirectional control procedure. (Reprinted with the permission of The Experimental Psychology Society from *Q. J. exp. Psychol.*, **42B**, 59–71.)

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.

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 Fig. 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; i.e. 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, observers tended to push the joystick in the same direction, relative to their own bodies, as had their demonstrators. 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 (C. M. Heyes, E. Jaldow, E. Ray & G. R. Dawson, unpublished data).

These studies indicate that budgerigars and laboratory rats are capable of non-vocal 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;

Hogan 1988; Heyes & Dawson 1990; Visalberghi & Frigaszy 1990a). Consequently, it would be wrong to assume without further, methodologically sound research that imitation is found only in budgerigars and rats, or even that it is rare within the animal kingdom. Until more is known about the phylogenetic distribution of the capacity for imitation, hypotheses regarding its adaptive function (e.g. Lefebvre & Palameta 1988), must remain largely speculative.

CULTURE

Some investigators assume that social learning and imitation are equally likely to produce 'traditions' (Morgan 1900; Mainardi 1980; Roper 1986) or mediate 'cultural transmission' (Menzel et al. 1972; Bonner 1980; Sherry & Galef 1984), but many argue or assume that there is a special relationship between imitation and culture (e.g. Washburn 1908; Piaget 1962; Huxley 1963; Bruner 1972, 1983; Lorenz 1974; Dawkins 1976, 1982; Munding 1980; Hull 1982; Boyd & Richerson 1985, 1988; Bandura 1986; Lefebvre & Palameta 1988; Masur 1988; Meltzoff 1988; Rogers 1988; Whiten 1989; Dennett 1990; Galef 1992). The latter view, that imitation is better able than social learning to support culture, appears to be based on two assumptions: (1) that imitation can, and social learning cannot, effect the transmission of information between social interactants; and/or (2) that imitation-mediated transmission can, and social learning-mediated transmission cannot, support stable behavioural traditions and the accumulation of information within a population (e.g. Boyd &

Richerson 1985; Lefebvre & Palameta 1988; Galef 1992). In what follows, I argue that both social learning and imitation can effect the transmission of information, and that neither is likely to be crucial in determining whether information can spread and accumulate within a population. Thus, both social learning and imitation can effect social transmission, and neither is a mechanism of cultural transmission.

Social Transmission

The idea that imitation, but not social learning, can effect information transmission seems 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 (Boyd & Richerson 1985). It is true that imitation is the only type of social learning that has been acknowledged by investigators to be resistant to explanations that do not refer to unobservable psychological processes. However, this phenomenon in the history of science does not indicate that imitation is alone in involving such processes, in being cognitive, and therefore, by implication, involving the acquisition of information (Heyes & Plotkin 1989). This is an empirical issue, and one that has been largely resolved in favour of the hypothesis 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 that 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 that 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 assume that this difference, in the conditions of learning, signifies a difference in the process of learning.

Thus, social learning and imitation are alike in involving the acquisition of information, but can they both effect information transmission? That is, in each case, do animals tend to acquire through interaction with a demonstrator, not just some information, but the information that guided the demonstrator's observed behaviour?

Although social learning consists of learning about the environment, rather than behaviour, through conspecific observation, it is apparent that both imitation and social learning allow, not only information about the environment, but also information about behaviour, to be transmitted between animals. That is, in both social learning and imitation, the fact that one animal possesses a certain piece of information about behaviour can play a significant, causal role in another animal acquiring the same information. The only difference is that in the case of social learning the potential receiver animal must not only observe the potential transmitter animal, but also act on its environment, in order to receive the message, the information about behaviour.

To illustrate these points, consider the results of some experiments showing that pigeons, *Columba livia*, can acquire a paper-piercing behaviour through conspecific observation. Palameta & Lefebvre (1985) allowed several pigeons to observe conspecific demonstrators piercing a hole in a sheet of paper covering a box of seed, and eating some of the food inside. The paper was white, with a red spot in the area towards which the demonstrators directed their pecks. When they were presented with a similar seed box, the birds that had observed the piercing and eating sequence were more likely to pierce the paper than were control birds that had observed piercing alone, eating alone, or neither piercing nor eating.

The birds that observed piercing and eating may have engaged in social learning or imitation, but either way they could have provided an example of social transmission of behaviour and of information about behaviour. If it was social learning, then the boxes joined by solid arrows in Fig. 2 represent a likely sequence of events. Before the experiment, the demonstrators had the information that pecking

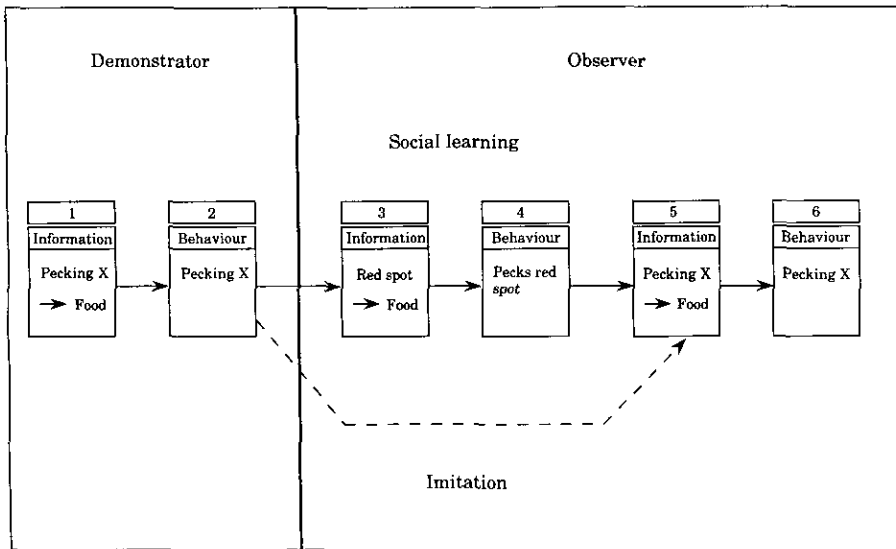


Figure 2. Schematic representation of the social transmission of information about a foraging technique through social learning and imitation.

the paper in a certain way, X (e.g. with a certain force, with its beak open to a certain degree) resulted in access to food (Box 1), and it was this information that made the demonstrators peck in the X way while being observed (Box 2). The demonstrators' action 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. Consequently, the observers acquired through observation alone some information about the environment, specifically information about the relationship between the red spot and access to food (Box 3; Hearst & Jenkins 1974; Heyes & Dawson 1990). This information led the observer pigeons to peck the red spot in a non-specific way (not in exactly the same way as the demonstrators, but in the way that pigeons peck almost any stimulus that has been associated with food; Box 4), and through trial and error learning initiated by this action, the observers may have acquired the information that was guiding the demonstrators' action (Box 5), and the precise behaviour exhibited by the demonstrators (Box 6).

If the observer pigeons instead engaged in imitation (the dashed arrow in Fig. 2), then the stages represented by Boxes 3 and 4 would have been missed out of the sequence. By definition, imitation involves the acquisition of information

about behaviour through observation of the behaviour alone. However, this difference between social learning and imitation in terms of the sufficiency of observation cannot justify a denial that both social learning and imitation can effect the transmission of behaviour (Boxes 2 and 6), and of information about behaviour (Boxes 1 and 5). In both social learning and imitation, interaction with an animal that has a certain piece of information or exhibits a certain behaviour may play a causal role in acquisition of the same information or behaviour by the observer.

In principle, then, both imitation and social learning can mediate behaviour and information transmission; they can both effect social transmission. The primary empirical evidence in support of this view comes from nearly 100 years of research that has failed to provide unequivocal evidence of imitation in non-human animals (for reviews see Roper 1986; Galef 1988; Whiten & Ham 1992). Each time data have been put forward as evidence of imitation, it has subsequently been discovered that they can be explained with reference to social learning; that after observation the observer animals may have behaved in the same way as the demonstrators because they had learned about the environment, rather than behaviour, while observing. This indicates that social learning has considerable potential to mediate behaviour and

information transmission. If this were not the case, then social learning and imitation would have proved much easier to distinguish empirically.

Cultural Transmission

In the literature on non-human animals, traditions tend to be defined with reference to the cause of population-specific behaviour. If a behaviour, B, is common among the members of one population, P, and rare or absent in another population, and if this difference is thought to have been caused, not by genetic or environmental variability between the groups, but by social transmission of the behaviour within P, then B is said to constitute a 'tradition' (Morgan 1900; Menzel et al. 1972; Mainardi 1980; Srivastava 1991; Galef 1992; Whiten & Ham 1992). Some investigations take all traditions, thus defined, to be 'cultural' phenomena, while others (e.g. Galef 1992; Tomasello et al., in press) assume that cultures, or the products of cultures, are a subset of traditions in which the focal behaviour, B, has been formed through 'the accumulation of modifications over time' (Tomasello et al., in press). According to this definition of culture, the potato-washing behaviour of Japanese macaques, *Macaca fuscata* (Kawamura 1959), for example, would be counted as traditional but not cultural. It would not be regarded as cultural because there is no reason to believe that the present form of the potato-washing behaviour is the product of high fidelity social transmission, not merely of the 'inventor's' behaviour, but of subsequent adaptive modifications to that prototype.

Two considerations favour the view that cultures should be distinguished from other traditions with reference to the accumulation of modifications. First, since accumulation of modifications is the fundamental process of biological evolution, this method of characterizing culture has a relatively firm theoretical base in the many promising attempts to develop evolutionary models of cultural change (e.g. Campbell 1974, 1983; Plotkin & Odling-Smee 1981; Boyd & Richerson 1985). Second, the human attributes (e.g. artistic, technological and scientific) that are described as 'cultural' in ordinary discourse, seem to be a good deal more complex than, for example, potato-washing and termite-fishing (Goodall 1986), and it is plausible that their greater complexity derives from the accumulation of modifications. For these reasons, it is usually helpful to distinguish cultural traditions

from others, in the manner set out in the previous paragraph. However, both when 'culture' is equated with tradition, and when it is defined in terms of the accumulation of modifications, imitation is no more likely than social learning to play an important role in supporting culture.

Fidelity of information transmission is required for culture, however it is defined. Trial and error learning on the part of population members threatens transmission fidelity by increasing the probability that information acquired by an individual through social transmission will have been modified under the influence of local (spatial and temporal) environmental variables, before it is re-transmitted to another individual. Consequently, a process mediating social transmission (e.g. social learning or imitation) could be said to play an important role in supporting culture only if it could promote transmission fidelity by insulating transmitted information from erasure and modification resulting from individual, trial and error learning. Only in this case could the process mediating social transmission usefully be described as a process of cultural transmission.

Information is not insulated from modification by local environmental variables in the course of its transmission through social learning. At the end of a social learning interaction, an observer has, by definition, acquired some information about the environment from a demonstrator, and it must then act on the world, engage in some individual learning, if it is to convert this into information about behaviour. If this episode of individual learning results in the observer having the same information about behaviour as that which guided the demonstrator's observed action, then social transmission has taken place. However, such transmission is far from inevitable, and the probability of its occurrence depends on local environmental variables.

For example, consider again the pigeons that observed a conspecific pecking a certain way, X, a red spot on a sheet of paper and eating seed from beneath. The observer birds may have learned during observation that the red spot was associated with food (Fig. 2, Box 3), and may subsequently have learned to peck the paper in the X way to obtain food (Boxes 5 and 6), but they may instead or in addition have learned to peck it another way, Y or Z. Precisely what they learned as a result of their observation-directed interactions with the seed container (Box 4) would be influenced, not

only by the demonstrators' example, but also by the 'affordances' of the container (Gibson 1979), and by the outcomes of the observers' previous interactions with similar objects.

Imitation is apparently better able to insulate information in the course of social transmission, because information about behaviour is acquired more 'directly' in the case of imitation (Dawkins 1976; Hull 1982; Boyd & Richerson 1985; Galef 1992; Whiten & Ham 1992). Since, by definition, an imitator does not have to interact with its environment in order to receive information about behaviour from a conspecific, there is less opportunity for environmental variables to intervene and affect what is learned at the acquisition stage. However, this is not enough to prevent local environmental variables from editing transmissions. To do this, information would have to be, not only acquired, but also retained and used 'directly'. It would have to be insulated, not only while animal B acquires the information from animal A, but also while it is retained by B prior to its re-transmission to animal C. Thus, if information acquired through imitation is as likely as information acquired through individual or social learning to be lost or revised as a result of the imitator's own interactions with its asocial environment, then imitation is no more likely than social learning to support culture.

There is little evidence bearing directly on this issue, but the available data suggest that, like other acquired behaviour, imitated behaviour declines or disappears when it has aversive consequences and when alternative behaviour is equally or more rewarding. For example, children who behave aggressively towards a doll as a result of observing that behaviour in an adult, will cease to do so if their aggressive behaviour is punished (Bandura & 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 a few responses, this tendency disappears, and both groups push predominantly to the left (C. M. Heyes, E. Jaldon, E. Ray & G. R. Dawson, unpublished data). 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 insulated from modification by the environment during retention. In principle, information acquired through imitation could be insulated, even if imitated behaviour is not, but I know of no evidence favouring this hypothesis. For example, I am not aware of any studies showing that behaviour initially acquired through imitation is more readily relearned than behaviour acquired through social learning, or that people give a more accurate verbal report of information acquired through imitation, even when they do not use it to guide their non-verbal behaviour. There is no *a priori* reason to anticipate such effects, and, even if they exist, it is unlikely that they would allow faithful transmission of information in non-human animals. 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 insular retention of information acquired through imitation could not support cultural transmission unless it were accompanied by insular retention of behaviour (Heyes, *in press a*).

If social learning and imitation do not insulate information in the process of social transmission, then any traditions (cultural or otherwise), any inter-population differences in behaviour that are typically acquired by social learning or imitation, are unlikely to exist because those behaviour patterns are so acquired. Some kind of social transmission process is necessary for a tradition to become established, but the availability of such a process, whether it is social learning or imitation, is so far from sufficient to establish a tradition that it cannot coherently be said to be responsible for the population-level effect. Consider, for example, dialect learning in song birds. What makes locale-specific song patterns possible is not the fact that song patterns can be acquired through imitation. The processes responsible are those that enable certain species to generate song variants that are arbitrary with respect to fitness (Lynch et al. 1989), to avoid exposure to alternative song types in adulthood and/or to resist the influence of other song types to which they are exposed (Petrinovitch 1988). It is these processes that promote faithful transmission.

More generally, the psychological processes that support culture are those that insulate socially transmitted information from modification through individual learning, that prevent or discourage individuals from 'testing' information acquired from conspecifics. They may include processes that allow individuals (1) to hold and transmit information about temporally and spatially remote objects and events or metaphysical entities, (2) to adhere to social norms or hold moral beliefs, and (3) to store information exosomatically. In the case of (1), testing may be impossible in practice or in principle, and in the case of (2), socially transmitted information may be insulated from change by an associated belief that it is morally good, or socially desirable to avoid modification (Dennett 1990). If socially transmitted information can be stored in a durable form outside the bodies of social interactants (3), it may remain available for retransmission in spite of having been tested and rejected by individuals (Rindos 1985). Each of these examples of processes that may support culture seems likely to operate in conjunction with a symbolic or instructional process of learning (Hull 1982; Hayes et al. 1986; Galef 1992). However, to the extent that culture depends on fidelity of social transmission in the face of local environmental fluctuations, the formation of cultural attributes is likely to depend crucially, not on processes of information acquisition (e.g. social learning, imitation and instruction), but on processes that contribute to faithful or 'blind' (Campbell 1974, 1983) information retention.

If the foregoing analysis is correct, then research on imitation in non-human animals has no direct or special bearing on 'the question of animal culture' (Galef 1992). Establishing whether the members of any given species are capable of imitation will not tell us whether they have cultural attributes, and thereby enable us to identify the evolutionary precursors, or phylogenetic origins, of human culture (Boyd & Richerson 1985).

COGNITION

In contrast, imitation of certain kinds of actions by animals has significant implications for our understanding of their cognitive capabilities. The actions in question are those that yield very different sensory inputs to an animal, Ego, when Ego performs them, and when Ego observes them being performed by another animal. This is the case for facial expressions and many whole body movements

(including cup cover removal by budgerigars; Galef et al. 1986; and joystick pushing by rats: Heyes & Dawson 1990; see Definitions and Evidence above), but not for vocal behaviour (Thorndike 1898; McDougall 1923). A human example is the whole body movement of curtsying. If I look down when I curtsy, I see something very different from what I see when I look across at somebody else curtsying. 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 tactile feedback from their own actions?

Thus, task analysis suggests that imitation is an especially demanding variety of visual-tactile cross-modal performance (Ettlinger 1960; Ettlinger & Wilson 1990; Meltzoff 1990; Rose 1990), of behaviour requiring an individual spontaneously to equate patterns of sensory stimulation in different modalities. However, it is unlike other cross-modal achievements in requiring an animal to equate topographically visual input from its environment with response-generated kinaesthetic and/or proprioceptive stimulation. These demands may or may not indicate that the processes underlying imitation differ from those mediating other cross-modal tests, such as transfer of a three-dimensional object discrimination from the visual to the tactile modality (Wilson & Shaffer 1963; Frampton et al. 1973), but at present all genuine examples of cross-modal performance in non-human animals are largely unexplained. There are several outstanding questions. Is the information derived from one modality coded in such a way that it can be directly transformed into the code for the other modality, or is there some mediating amodal code? What kind of sensory codes would permit direct transformation? What kind of amodal code could be used by a non-linguistic animal? When does the transformation occur, automatically during receipt of information in the first modality, or later and only under certain conditions? If the latter, what triggers or provokes transformation? The significance of imitation lies in the fact that, in attempting to answer these and similar questions, we may find that animals can manipulate and transform information in ways that have hitherto been assumed to be way beyond their capabilities.

It is widely recognized that imitation is a potentially important clue in unravelling animal mentality, intelligence or cognition, but the foregoing account of what makes imitation special in this regard differs somewhat from other published proposals. The most prominent of these suggest that imitation implies 'self-consciousness' (Thorpe 1956; Gallup 1982), 'representation' (Meltzoff 1990), 'purpose' (Morgan 1900; Thorpe 1956; Kohler 1959; Galef 1988), and 'metarepresentation': the capacity to attribute mental states to other animals (Whiten & Byrne 1991; Whiten & Ham 1992; Byrne, in press; Tomasello et al., in press).

If 'self-consciousness' is taken to mean merely the capacity to distinguish sensory input generated by one's own body from that originating elsewhere, then imitation does indeed imply self-consciousness. An individual could hardly map visual input from another animal's behaviour onto feedback from its own actions if it could not distinguish the latter from the former and from other extrinsic input. However, if self-consciousness is defined in this minimal way, imitation is not unusual in providing evidence that non-human animals are self-conscious. The capacity to distinguish extrinsic sensory input from feedback is implied by such common feats as avoidance of collision with objects during locomotion. If, on the other hand, self-consciousness is taken to be phenomenal awareness of an existential 'I' (Gallup 1982), then it is not clear that any behavioural data could provide persuasive evidence of such an ultimately private condition, or why imitation should be singled out as especially suggestive in this regard (see Heyes, in press b for a review).

To defer imitation, to copy a novel act when it is no longer visible, an individual must be capable of 'representation', of forming and storing a cognitive record of the act observed (Meltzoff 1990). However, deferred imitation is far from unique in requiring this capacity, and there is now ample evidence that it is present in many non-human animals. One example was described above (Holland 1981). Others are provided by studies showing that rats, pigeons and monkeys can readily learn to solve delayed conditional discrimination problems in which they must remember the identity of a stimulus presented at the beginning of a trial in order to choose correctly which response to make at the end of the trial (e.g. D'Amato & Worsham 1972; Grant 1976).

Imitation would be purposive (Morgan 1900; Thorpe 1956; Kohler 1959) or 'goal-directed' (Galef 1988) if, when an observer copies the movements of a demonstrator, its actions are regulated by a representation of their potential outcome (e.g. Millikan 1984). For example, an animal that imitates a foraging technique may do so with the purpose of obtaining food of the kind consumed by the demonstrator. To find out whether any given example of imitative behaviour is regulated in this way, it would be necessary to manipulate the value of the outcome for the observer (Heyes & Dickinson 1990). If the imitative behaviour is goal-directed, one would expect it to occur only when the outcome for the demonstrator is one to which the observer assigns a positive value. If imitation also occurs when the outcome has a negative value for the observer, then the imitative behaviour is likely to be automatic, rather than purposive.

I do not know of any studies that have sought evidence of goal-directed imitation in animals. However, Darby & Riopelle (1959) found evidence of goal-directed social learning in an experiment in which rhesus monkeys observed a conspecific demonstrator choosing one of two objects before being allowed to choose between two similar objects themselves. Although the observer monkeys were rewarded regardless of the choice that they made, if the demonstrator's choice had been rewarded, they tended to choose the same object, but if it had been unrewarded, they chose the other object. Further evidence that non-imitative behaviour can be goal-directed has been provided using 'reinforcer-revaluation' procedures with rats (Dickinson & Balleine 1990; Heyes & Dickinson 1990). For example, rats that had learned to press a lever for dry food pellets and to pull a chain for sucrose solution when hungry then pressed the lever less when thirsty than rats that had, before switching from hunger to thirst, learned to press the lever for sucrose solution and to pull the chain for dry food pellets. The frequency of the lever-pressing action was sensitive to a shift in the value of the outcome for the animals, implying that execution of the action was regulated by a representation of its outcome, that it was goal-directed. Thus, imitation is not necessarily purposive, and even if further research shows that imitation is often, or even always, goal-directed it will not be the first to indicate that animals can behave in this way.

Finally, imitation may involve 'metarepresentation' (Whiten 1989; Whiten & Ham 1992; Byrne,

in press) but there is no compelling reason to believe that it does. An imitator may represent the imitated animal's mental state, its point of view, or its beliefs and desires, but this kind of higher-order representational ability is not implied by the act of imitation. What is apparently essential for imitation is that the imitating animal represent what the demonstrator did, not what it thought. The view that imitation does, as a matter of fact rather than necessity, involve metarepresentation, hinges on two assumptions: that apes can, and monkeys cannot, imitate; and that apes have, and monkeys have not, provided other evidence of the capacity to attribute mental states. Both of these are weak given that putative evidence of imitation in apes is widely contested and almost exclusively anecdotal (e.g. Kitahara-Frisch & Norikoshi 1982; Mitchell 1987; Tomasello et al. 1987; Galef 1988; Visalberghi & Frigaszy 1990a, b), and that neither observational nor experimental techniques have revealed other behavioural phenomena clearly indicative of mental state attribution (Heyes 1993, in press c). On the other hand, there is evidence that, contrary to a formerly dominant view (Piaget 1962), imitation and meta-representation are not intimately connected in human ontogeny. Infants are able to imitate months or even years before they are able, for example, to appreciate that another child may have a false belief (Leslie 1987; Meltzoff 1988, 1990).

In summary, imitation may or may not involve the kinds of cognitive states and operations that are characterized as self-consciousness, purposiveness and mental state attribution. These possibilities are fascinating, but in advance of further research, they must be regarded as remote, and they do not relate to imitation's special, if not unique, significance. There are other, easier ways of finding out whether animal action is goal-directed or guided by meta-representation, and research on imitation is no more likely than research on other forms of social learning to reveal the phylogenetic origins of culture, but it may tell us a great deal about how non-human animals form and transform representations of action.

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