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What Is the Significance of Imitation in Animals?

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I. INTRODUCTION

For at least a century, and with increasing rigor and sophistication in recent years, psychologists and biologists have investigated whether nonhuman animals (henceforward "animals") are capable of a certain kind of social learning, namely, imitation (Thorndike, 1898; Galef, 1988; Tomasello, 1996; Tomasello *et al.,* 1993b; Whiten and Ham, 1992). Imitation consists of response learning by observation, i.e., learning how to move the body by observing the behavior of others. Other varieties of social learning consist of stimulus learning by observation; these are means of acquiring information about the static or dynamic properties of objects; about their value, location, and motion (Heyes, 1994).

Although this article includes a survey of some of the most interesting recent experiments on imitation in animals, our main purpose is not to address the question "Can animals imitate?" Instead, we offer an answer to a related and somewhat neglected question. What is the significance of imitation in animals; what would be the advantage of knowing whether animals are capable of response learning by observation? We will argue that the principal significance of this field of animal behavior research lies in what it can reveal about the cognitive mechanisms underlying imitation in humans and animals; specifically, that it has the potential to establish whether those mechanisms are "transformational" or "associative."

The greatest challenge for any theory of the cognitive mechanisms of imitation is to explain imitation of "perceptually opaque" actions, those actions which yield dissimilar sensory inputs when observed and executed. Section II explains why this is difficult, and Section III distinguishes two types of theory of imitation, transformational and associative, in terms of the way in which they attempt to meet this challenge. Although it is fairly clear whether each existing theory postulates transformational or associative processes, the models currently available are not specified in sufficient

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detail to allow empirical testing of conflicting predictions. Section IV sketches a new, associative sequence learning (ASL) theory which is more amenable to empirical testing, and Section V discusses the kind of evidence of imitation in animals that would favor this theory over transformational alternatives or vice versa. In Section VI we search for this kind of evidence among recent experiments on imitation in animals using two-action test procedures, and in Section VII we consider briefly the significance of imitation in animals with respect to culture rather than cognition.

II. Perceptual Opacity

All behaviors or actions may be said to lie on a continuum of perceptual opacity; they vary in the degree to which they yield dissimilar sensory inputs when observed and executed (Fig. 1). Highly perceptually opaque actions, which usually generate highly dissimilar sensory inputs, include head movements and facial gestures. For example, under typical observation conditions, when a human observer (O), sees another person, a "demonstrator" (D), raising an eyebrow, the sensory input to O is primarily visual and includes the movement of an arc (the eyebrow) in the upper portion of an elliptical frame (the face). In contrast, when O raises his own eyebrow, the sensory input to O is primarily kinesthetic, the movement is felt rather than seen, with any visual component consisting largely of an increase in the amount of light entering one eye. Perceptually transparent movements, those which are low on the dimension of perceptual opacity, yield relatively similar sensory inputs when observed and executed and typically include distal appendage movements and vocalizations. For example, although O receives kinesthetic input when he fans his fingers and not when he observes D performing the same finger movements, the pattern of visual input to

Perceptually Opaque   Perceptually Transparent

High   Discrepancy between sensory inputs   Low
                  during observation and execution

Head movements   Distal appendage movements
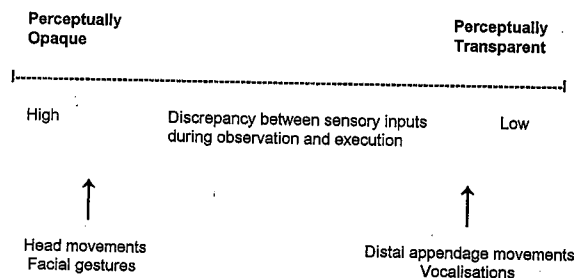Facial gestures   Vocalisations

FIG. 1. Summary of the discussion of perceptual opacity, a new, imitation-relevant dimension of action.

O is very similar in the two cases, especially when O stands behind or alongside D while observing.

Perceptual opacity is not an invariant property of an action. It can vary with observation conditions, including the spatial orientation of O's sense organs in relation to D and to the part of O's body that moves during action execution, and via the use of instruments such as mirrors and video recorders. For example, mirrors and manual, tactile exploration of D's and O's body by O can render highly transparent actions, such as facial gestures, that are normally highly opaque.

Imitation of perceptually opaque actions is more difficult to explain than imitation of perceptually transparent actions because in the former case it is not clear how O could derive the information necessary to produce a behavioral match. In principle, imitation of perceptually transparent actions could be achieved through a sensory matching process in which O generates variant actions, compares the sensory feedback from these "trials" with a concurrently present or memorial sensory representation of D's action, and selects the variant(s) for which the discrepancy is minimal. However, a simple sensory matching process such as this cannot explain imitation of more perceptually opaque actions.

In recognition of what we are calling the problem of perceptual opacity, Thorndike (1898) argued that "motor imitation" is a more impressive cognitive feat than "vocal imitation," and Piaget (1951) suggested that imitation of "invisible" movements represents a later stage in cognitive development than imitation of visible actions such as finger movements. The dimension of perceptual opacity subsumes these earlier distinctions and may be more helpful in the development of an adequate theory of imitation for two reasons. First, unlike Piaget's distinction, it draws attention to the fact that a simple sensory matching hypothesis is insufficient to explain imitation not only of actions without visual feedback but also of those which yield different visual inputs when observed and executed. Second, and in contrast with Thorndike's distinction, it acknowledges that sensory matching can explain imitation of some nonvocal behaviors, and that this depends both on the body parts involved in the action and on the observation conditions such as viewing angle. Thus, the problem confronting theories of imitation, the problem of perceptual opacity, is broader than the visible/invisible distinction implies, narrower than the motor/vocal distinction implies, and may be more accurately described by a dimension than a dichotomy.

III. Theories of Imitation

Investigators of imitation in animals seldom refer to any explicit theory of imitation, and it is therefore surprising that at least a dozen such theories

have been elaborated in modern terms and some significant degree of detail. We divide these theories into two groups according to whether they attribute imitation to transformational or associative psychological processes. Generally, associative theories (e.g., Allport, 1924; Aronfreed, 1969; Gewirtz, 1971; Holt, 1931; Miller and Dollard, 1941; Mowrer, 1960; Skinner, 1953) claim that the information required to produce an imitative match between the behavior of an observer and that of its demonstrator (or model) is derived from experience. They suggest that the capacity to imitate a given action, *X*, now, derives from experience of simultaneously observing and executing *X* in the past. In contrast, transformational theories (e.g., Bandura, 1986; Meltzoff, 1990; Piaget, 1951) assert that a substantial portion of the information necessary to produce a behavioral match is internally generated by complex cognitive processes. These processes transform the sensory input from the demonstrator's action into a "symbolic conception" (Bandura, 1986), "imaged representation" (Piaget, 1951), or "supramodal representation" (Meltzoff, 1985) which contains the information necessary to guide execution of matching behavior by the observer.

Associative and transformational theories represent two important, plausible, alternative accounts of the processes underlying imitation. However, each existing theory has shortcomings which make it unsuitable as a framework for empirical investigation of whether, or to what extent, associative and transformational processes mediate imitation. A problem common to transformational theories is underspecification. They do not indicate how information in sensory input from the demonstrator is transformed into a representation capable of guiding production of matching behavior. In other words, although transformational theories claim that, even for perceptually opaque actions, the observer's information processing system can translate sensory input from the demonstrator into a production code, they do not give any hint of the mapping functions involved.

For example, Bandura's (1986) "social-cognitive" theory suggests that information obtained during observation of a demonstrator's action is first stored as a sensory representation and then transformed into a "symbolic conception" which "provides the internal model for response production and the standard for response correction." In other words, the symbolic conception can both generate motor programs for approximately matching behavior and edit these programs to produce more precisely matching behavior using sensory feedback from action execution. Thus, Bandura's theory suggests a three-part cognitive architecture for imitation consisting of a sensory representation, symbolic conception, and motor program; however, it is silent regarding the process or mechanism by which imitation of perceptually opaque actions is achieved. It does not say how a sensory

representation is converted into a symbolic conception capable of minting motor programs for matching behavior.

As a consequence of their underspecification, transformational theories do not make predictions about the conditions of imitation—about which actions can and cannot be imitated, under what observation conditions, and by which species or individuals—and this, in turn, makes them resistant to empirical evaluation.

Associative theories have a variety of weaknesses. For example, Mowrer's (1960) two-factor theory and Aronfreed's (1969) template theory postulate sensory matching processes, and the authors apply them only to perceptually transparent actions. This may be interpreted as an implicit prediction that perceptually opaque actions cannot be imitated. If so, it seems that these theories are falsified by the common experience that adult humans can, for example, imitate facial expressions. If not, two-factor theory and template theory are radically incomplete because they simply do not address the question of how perceptually opaque actions are imitated.

Holt's (1931) associative theory is more clearly inconsistent with what is known about human imitative competence. Holt suggested that the capacity to imitate is acquired through social interactions in which an adult faces a child and mirror imitates the child's actions. For example, when the child moves his right arm to the right of his body, the adult moves her left arm to the right of the child's body. The child's gaze follows the adult's imitative movement and thus, according to Holt, the child associates the stimuli that initiated his own movement (nature unspecified) with sensory feedback from visual tracking to the right of his body. As a consequence of this association, the child will subsequently respond to sight of a demonstrator's arm moving toward the right of the child's visual field with an arm movement to the same location in space.

Holt's theory is ingenious, but it makes the false prediction that humans will be incapable of transposition imitation, e.g., imitating right arm movements with their right arm, not their left, when they are facing the demonstrator. To achieve this capacity under the conditions and via the mechanisms specified by Holt's theory it would be necessary for adults regularly to imitate the actions of infants while the adults have their backs turned to the infants. In fact, humans are capable of transposition from age 7 or 8, and this mode of imitation is preferred to mirroring from approximately age 14 onwards (Gordon 1922/1923; Heyes *et al.*, 1999; Wapner and Cirillo, 1968).

Other associative theories, like transformational theories, are untestable as a result of their underspecification. Miller and Dollard's (1941) copying theory (not to be confused with their matched-dependent theory) has this problem, and since it is probably the most fully elaborated account of

imitation to date it is worth considering in some detail both the postulates and the key weaknesses of copying theory.

Using the example of a person being taught to sing, Miller and Dollard's (1941) copying theory offered an account of how this O is able to match any note, or sequence of notes, sung by another person. In stage 1 of training to match a single note (e.g., C), the demonstrator/teacher detects sameness and difference cues and O responds to them randomly. Thus, when O voices a note higher or lower than C, the teacher says "No" or "That's wrong"; this makes O feel anxious and initiates random variation in the note he is producing. When O finally hits on C, the teacher says "Yes" or "Good," and the learner feels relieved. In stage 2, the teacher says "Too high" or "Too low" when O is producing the wrong note, and O responds directionally by producing a higher or lower note.

In stages 3 and 4, O becomes able to detect the sameness and difference cues. When the trainer says "No," "Yes," "Too high," or "Too low," O repeats these words to himself and then experiences the twinge of anxiety or feeling of relief originally provoked by the trainer's utterance. The learner's implicit repetition of the words occurs in close temporal proximity to reinforcement (an increase or decrease in anxiety) and therefore, according to Hullian learning theory, these responses become "anticipatory"; they begin to occur in direct response to the sameness and difference cues. After some practice guided by direct detection of the sameness and difference cues, the learner will be able to match a C reliably at first attempt, and he can then move on to other notes. Miller and Dollard (1941) asserted that it would be easier for the learner to match each successive note attempted in training because the sameness and difference cues would have something in common with those of previous notes in the sequence, and therefore "generalization" would occur.

Having learned to copy every single musical note in stage 5, in stage 6 O learns, through the processes described for stages 1–5, to copy sequences of notes. Stage 6 learning is facilitated, via generalization, by prior training to match single notes. After learning to match an unspecified range of sequences, Miller and Dollard (1941) claimed that the one-time novice would be an expert capable of copying without practice novel sequences of notes.

Copying theory has several virtues relative to earlier theories of imitation, but it also has two significant weaknesses—the first distinctive and the second in common with some other associative theories that assign an important role to reinforcement (Gewirtz, 1971; Gewirtz and Stingle, 1968; Miller and Dollard, 1941; matched-dependent theory). The distinctive weakness relates to Miller and Dollard's claim that, at stage 3 in learning to copy, O's behavior comes under the direct control of

sameness and difference cues via repetition of D's instructions by O. This implies that before an O can learn to copy any other actions, he or she must be able to copy, albeit implicitly, D's instructions—the behavior through which Ds communicate whether a putative imitation is right or wrong. If this is the case, however, how do Os achieve this initial feat of imitation? How do they come to be able to copy the instructions themselves?

The second problem with copying theory is that it assigns a critical role to generalization without specifying dimensions of generalization. This problem is almost immediately apparent in other reinforcement theories, but it is concealed in Miller and Dollard's (1941) copying theory because their exposition deals almost exclusively with imitative singing of musical notes. Actions in this domain (e.g., "singing C" and "singing D") have two unusual properties: (i) They are defined, differentiated one from another, in terms of their sensory consequences rather than the effectors involved, and (ii) the sensory consequences that define the actions can be ordered on a known scale. These features of singing are important because, in combination, they make it plausible that generalization would, for example, make it easier to learn to copy a D than an E note after learning to copy a C. It is possible to specify the psychophysical dimensions on which the sameness cue DD is more like CC than is EE and on which the difference cue DB is more like CB than is EB. However, most actions cannot be ordered on a scale (or at least we do not know the scale on which they can be ordered) and therefore, for most actions, the claim that there is generalization of learning to copy could be tested only on the basis of ancilliary hypotheses about generalization gradients; currently, these would be very difficult even to formulate.

Consider, for example, a person who has been trained to copy a curling movement of his or her left index finger and is now learning to copy a curling motion of the left ring finger. Will this person's prior training help him or her, via generalization, more or less than if it had involved imitation of a curling movement of the right ring finger, a curling movement of the third toe on either foot, or a rigid, up and down movement of the left ring finger? Because the action "curling a finger" is not part of a known scale, copying theory does not make any obvious predictions.

Skinner (1953) provided a sketch of an associative, reinforcement-based theory of imitation which does not use the concept of generalization but, unfortunately, suffers from underspecification. Skinner suggested that in order to imitate an action now, such as a dance step, O must have performed the very same dance step in the past and been rewarded while observing the dance step performed by a D. This means that imitation, response learning by observation, is impossible, and that an

individual cannot expand his or her behavioral repertoire through action observation. However, Skinner implied through one of his examples that novel sequences of actions can be acquired through observation. Thus, he suggested that a skilled dancer who has previously learned to imitate each step in a dance sequence can copy the whole sequence when it is demonstrated by an instructor. This would be latent, or "behaviorally silent" learning (Dickinson, 1980) (learning without action), and therefore it would be inconsistent with Skinner's behaviorist analysis of learning. Therefore, it is perhaps not surprising that he did not suggest a mechanism through which it could be achieved.

IV. Associative Sequence Learning Theory

In the preceding section, we argued that existing theories of imitation successfully delineate two kinds of processes (transformational and associative) that could mediate imitation, but that none of these theories are couched in a way that makes it possible to test empirically whether, or to what extent, transformational and/or associative processes are responsible for imitation in the real world. In this section, we outline a new ASL theory of imitation which incorporates components from several preceding associative models. The principal purpose of ASL theory is to stimulate the development of other theories (associative and transformational) that are (i) consistent with what is already known about the conditions of imitation and (ii) sufficiently well specified to generate testable predictions. We hope that ASL theory meets these conditions, but we would be very surprised if it turned out to provide a fully accurate account of imitation.

A. Action Units

ASL theory is schematically represented in Fig. 2. It assumes that, rather than being unitary, the vast majority of actions comprise sequences of component actions or "action units." Thus, although it is conventional to think and speak of "an action" being imitated, ASL assumes that it is always a sequence of action units that is imitated. The hand icons at the top of Fig. 2 represent a sequence of hand movements: pointing, followed by splaying the fingers, followed by a victory sign. We use this action sequence for illustrative purposes, but two considerations should be borne in mind. First, the action units involved in any given case of imitation may be smaller (e.g., closing one finger toward the palm) or larger (e.g., incorporating pointing and splaying). Second, ASL theory applies to rela-
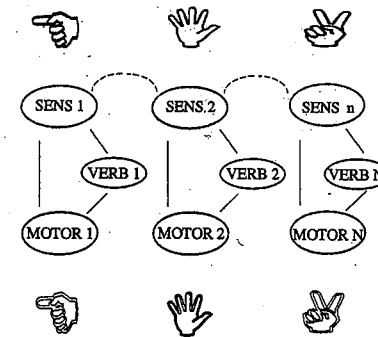
Fig. 2. Schematic representation of the associative sequence learning theory of imitation learning.

tively perceptually opaque actions such as facial expressions as well as to relatively perceptually transparent actions such as hand movements.

B. Horizontal Processes

Suppose that an observer sees the set of hand movements in Fig. 2 (point, splay, and victory) for the first time, i.e., the sequence is novel. ASL theory suggests that two sets of associative processes, resulting in "horizontal" and "vertical" links, determine whether and to what extent the observer will be able to imitate the sequence. Through the horizontal processes, associations are formed which link sensory, in this case visual, representations of the action units in the sequence ($SENS_{1...n}$). These visual representations may be associated with one another in a chain such that, for example, activation of $SENS_1$ activates $SENS_2$ directly, but studies of list learning in humans have shown that such chaining models seldom apply (Henson et al., 1996). It is more likely that the horizontal processes conform to a context-based model (Brown, 1997) in which sensory representations of successive action units become associated with successive states of a time-varying context or control signal, such as the output of an internal clock. This distinction between chaining and context-based horizontal association is not crucial for the present purposes, but the lines connecting sensory representations in Fig. 2 are dashed and curved to signify that context-based association is more likely to occur.

Through the horizontal processes, the observer could be said to learn what the action sequence "looks like"; the O learns a stimulus sequence.

For example, if the observer were given a jumbled set of cards, each showing an action component (Carroll and Bandura, 1982), he or she would be able to pick out the components that appeared in the sequence and put those cards in the appropriate order. However, the horizontal processes are not unique to imitation (formation of visual representations, and their association with one another, proceeds as in other cases in which the individual learns a sequence of visual stimuli), and they are not sufficient to enable the observer to reproduce the novel action sequence. For imitation of the observed action sequence, the vertical processes are also necessary.

C. VERTICAL PROCESSES

The vertical processes operate before the novel sequence is observed and result in a sensory representation of each action component (e.g., $SENS_1$) becoming associated with a motor representation of the same component (e.g., $MOTOR_1$). ASL theory makes minimal assumptions about the content of motor representations. They may encode kinesthetic feedback from performance of the action unit and/or a motor program. What is important is that ASL assumes that a motor representation of an action unit can be formed only through performance of that unit, and therefore that the functioning of the vertical processes is such that the accuracy of imitative performance is directly related to the proportion of the components in an action sequence executed prior to sequence observation.

Vertical processes can result in sensory and motor representations becoming associated directly or indirectly. Direct associations are formed when an action unit is contiguously observed and executed (seen and done). There are three major sources of such experience: self-observation, mirrors, and synchronous action. Self-observation provides the kind of contiguous experience that will support imitation only for relatively perceptually transparent actions. For example, when an observer looks at her hand while moving her fingers, she receives contiguous experience of seeing and doing the finger movements. Mirrors and synchronous action (i.e., performing the same action at the same time as another individual) provide contiguous experience of observing and executing perceptually opaque and perceptually transparent actions. Behavioral synchrony may result from imitation of the observer by the model or simultaneous responding to a common environmental stimulus.

Indirect links between sensory and motor representations of the same action unit are formed when a second stimulus, distinct from sensory input arising from observation of the action unit, is consistently paired on some occasions with sensory input from the action unit and on other occasions

with performance of that unit. This is the "acquired equivalence" route (Hall, 1996) to imitation, and in humans the second stimulus is usually a word or phrase ($VERB_{1...n}$).

D. SUMMARY OF ASL THEORY

ASL theory suggests that imitation consists of the reproduction of a succession of action units, the sequence of which is novel—i.e., that prior to imitative performance, O has not executed the action units in the modeled order. It postulates that two sets of associative, contiguity-based processes are necessary for imitation. The horizontal processes operate during observation of the novel action sequence and do not require any overt action on the part of the observer. Hence, this is an associative but not a behaviorist theory. The horizontal processes (which also operate when information is acquired about the serial order of nonaction stimuli) mediate observational (i.e., behaviorally silent; Dickinson, 1980) learning of what the sequence looks like, but are not sufficient to support imitation. Reproduction of the action sequence will be possible to the extent that sensory representations of the sequence components have become associated, via vertical processes, with motor representations of the same components. Associations of this kind are formed when, in the course of self-observation, mirror exposure, and/or synchronous action, the observer contiguously observes and executes an action unit, or they are formed through acquired equivalence training (i.e., experience in which observation and execution of an action unit have each been paired with a common stimulus such as a word or phrase). To the extent that such vertical links have been formed, exposure to the novel action sequence, or recollection of that sequence mediated by the horizontal processes, will activate motor representations in the order appropriate for sequence reproduction (i.e., imitation). This activation gives the learner the potential to imitate the observed action sequence (represented by the bottom row of icons in Fig. 2)—the information necessary to reproduce the action sequence.

E. LEARNING AND PERFORMANCE

It is important to note that ASL theory is a theory of learning and not of performance. It specifies inputs and processes which result in an observer being able to imitate a novel sequence of action units, but just because the observer can imitate does not necessarily mean that he or she will imitate. Performance will be governed by additional motivational processes. However, just as there is no reason to suppose that distinctive perceptual and attentional mechanisms operate on sensory input from body movement

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interactant steps backward with the left. There is no convenient term for systematically nonmatching behavior of this kind, but that does not necessarily mean that it is infrequent or of little functional significance relative to imitation. Its relative obscurity may be due instead to its being more difficult to detect than imitation.

Second, the ASL definition is compatible with two time-honored definitions of imitation: Thorndike's (1898) characterization of imitation as learning "to do an act from seeing it done" and Thorpe's (1956) definition of "true imitation" as "the copying of a novel or otherwise improbable act or utterance." Rather than contradicting these definitions, the ASL view merely adds specification of the dimension of novelty—of the content of what is learned about the act from seeing it done (i.e., the sequence of the action units). However, ASL theory is inconsistent with a common interpretation of Thorpe's definition, which states that imitation refers to cases in which a completely novel action (whatever that might mean) is acquired through observation. ASL theory implies that this interpretation circumscribes an empty set of behavioral phenomena; that actions the components of which have not previously been executed, and executed during contiguous observation of the same act or in the context of acquired equivalence training, cannot be reproduced on the basis of information acquired through observation.

Third, like Thorpe (1956), ASL theory distinguishes imitation from "social facilitation." Imitation occurs when an observer reproduces a novel sequence of action units as a result of learning vertical associations between sensory and motor representations of the units and horizontal associations between sensory representations of successive units. By contrast, in cases of social facilitation, the sequence is not novel (e.g., the observer has previously observed and executed the target sequence as a whole), or experience does not play a significant role in formation of the horizontal and vertical associations mediating response reproduction. In the latter case, the associations are "hardwired" or, as Meltzoff (1990) stated, response reproduction is mediated by an "innate releasing mechanism."

Finally, ASL theory does not support a distinction between imitation and "reflexive" reproduction of a novel action sequence. The terms "mimicry" (Aronfreed, 1969) and "response facilitation" (Byrne and Tomasello, 1995) are sometimes used to refer to hypothetical cases of reflexive reproduction of a novel action sequence and to distinguish these from imitation, which is then defined as a goal-directed phenomenon. Because ASL theory focuses on learning rather than performance (see Section IV,E) it elides this distinction, emphasizing instead that, whether or not it is goal directed, imitation occurs through complex cognitive processes. They are complex by virtue of involving horizontal and vertical associations, in addition to the myriad

perceptual and motor functions involved in parsing and producing action sequences, and cognitive in the sense of being "behaviorally silent" (Dickinson, 1980)—not directly observable in behavior.

V. PREDICTIONS AND THEORY TESTING

Even in its current rudimentary form, ASL theory makes testable predictions. The two principal predictions are that imitation, reproduction of a novel sequence of actions, will be possible to the extent that the observer (i) is capable of stimulus sequence learning (i.e., learning what an action sequence looks like) and (ii) has contiguous experience of observation and execution of components of the action sequence or experience in which observation and execution have each been paired with a common (e.g., verbal) stimulus. If these predictions are inconsistent with the evidence, it suggests that ASL theory is wrong, and that different associative processes, or transformational processes, mediate imitation. If they are fulfilled, it would not necessarily indicate that ASL theory is correct, but it would strengthen its position relative to other untested and untestable theories.

The second, and more distinctive, of ASL theory's two principal predictions can be tested more readily through research on animals than in human experiments. This is because empirical evaluation of ASL theory requires experimental control of participants' previous experience of correlated observation and execution of units in the to-be-imitated action sequence, and this is very difficult to achieve for human subjects. For example, Ishikura and Inomata (1995) provided one of many demonstrations that humans are capable of response learning by observation in an experiment in which adult subjects were instructed to reproduce a sequence of seven balletic poses, demonstrated by a trained dancer. The Os were successful in carrying out these instructions and, since there was a close topographic match between the Os' and the Ds' behavior and the actions were not directed toward an environmental object, unlike most putative imitation in animals, this success could not have been due to the Os having learned by observation something about the static or dynamic properties of an environmental object. Thus, Ishikura and Inomata's participants provided evidence of response learning by observation but, since it would be practically impossible to assess the extent of their past experience of seeing-and-doing components of the sequence, their experiment does not provide a basis for testing ASL theory.

Training experiments, in which Os are given varying degrees of experience of seeing-and-doing action components before an imitation test, are likely to provide the most effective means of testing ASL theory, but these

would be laborious with human participants. The training phase would need to be long and/or intensive enough to prevent masking of its effects by prior, spontaneous experience of a similar kind. This problem can be minimized in research with many animal species by witholding until the experiment begins the opportunity to see, do, and see-and-do components of the to-be-imitated action.

Training studies of two types could be used to test ASL theory. In the first type, the target, to-be-imitated action would be "sequentially novel" for all subjects (i.e., it would consist of action units in a sequence that had not previously been observed or executed by any subject), whereas the extent to which the target action is "combinatorial novel" would vary across groups. The combinatorial novelty of an action for an O is inversely related to the proportion of the action's components which the O has contiguously observed and executed (or which have acquired equivalence through pairing with a third stimulus). If the proportion is low, the action has high combinatorial novelty for the O, and if the proportion is high it has low combinatorial novelty for O. For example, some observers would have prior experience of contiguously seeing and doing each of the components in the test sequence (low combinatorial novelty), others would have this experience for some but not all units (medium), and others would have no such experience (high). In this type of experiment, ASL theory would predict better imitative performance in the low group than in the medium group and the worst performance in the high group.

The second type of training experiment would vary not the degree but rather the kind of pretest experience of correlated observation and execution of action units. Thus, before observing a set of units in a novel sequence, AABBAA, some subjects would have correlated experience of seeing A and doing A, seeing B and doing B (group AA/BB), whereas others would see A while doing B and vice versa (group AB/BA). A control group would see and do, A and B as often as the other two groups, but observation and execution would be uncorrelated. ASL theory would predict that, after observation of the target sequence, group AA/BB would execute a sequence more like AABBAA than that of controls, whereas group AB/BA would perform a sequence more like BBAABB than that of controls.

To our knowledge, neither of these two types of experiment have been conducted with any species, and therefore the predictions of ASL theory have not been tested directly. However, within the existing literature on imitation in animals there may be evidence that is inconsistent with ASL and/or experimental paradigms (i.e., species and method combinations) that could be used in the future to test ASL theory directly. Evidence inconsistent with ASL would suggest that animals are capable of learning to perform a relatively perceptually opaque action by observation of that

action (i.e., response learning by observation) without prior experience of contiguously observing and executing the whole action or a significant proportion of its components (i.e., when the action is combinatorially novel). For future use in testing ASL theory against alternative models, an experimental paradigm needs to be reliable and accessible; it should reliably yield evidence of response learning by observation and be accessible in the light of ethical and cost considerations. In the next section we seek evidence of this kind: studies of imitation in animals which demonstrate response learning by observation when the test behavior is combinatorially novel or the procedure is reliable and accessible.

VI. SURVEY OF TWO-ACTION TESTS

In approximately the past 10 years, the use of two-action tests has substantially increased the rigor of research investigating imitation in animals. These tests are designed to isolate response learning by observation (imitation) from stimulus learning by observation, and they typically begin with observers being exposed to a demonstrator operating on a single object in one of two different ways. After this observation experience, each subject is given access to the object, and a record is made of the number of times he or she responds to the object using the same action as the demonstrator and using the alternative action, the one that he or she did not observe. A bias in favor of the former, of demonstrator-consistent responding, is prima facie evidence of imitation.

The current survey is confined to experiments using the two-action method because compelling evidence of the kind we are seeking (see Section V) is most likely to come from these. For convenience, studies of nonhuman primates (henceforward "primates"), rodents, and birds are considered separately. This categorization does not imply that there is sufficient evidence even to speculate about the phylogenetic distribution of the capacity to imitate.

A. PRIMATES

Whiten and colleagues conducted a series of two-action tests with chimpanzees (*Pan troglodytes*) (Whiten *et al.*, 1996; Whiten, 1998) and capuchin monkeys (*Cebus apella*) (Custance *et al.*, 1999) using a puzzle box or "artificial fruit." In the most recent of these studies (Whiten, 1998), four chimpanzees observed a human demonstrator removing two pairs of objects from the exterior of a transparent box containing food. The objects in each pair were situated close together and at some distance from the other pair. The

objects in one pair were bolts and in the other pair were T-bars. Two of the chimpanzees observed bolt removal followed by T-bar removal, whereas for the other two animals the T-bars were removed first. One chimpanzee in each of these conditions saw the bolts twisted and pulled out of position and the T-bars spun or turned, whereas the other animal saw the bolts poked out of their lodgings and the T-bars spun or turned. When given access to the objects, the chimpanzees showed a tendency to approach the objects in the observed sequence (e.g., those that observed bolt removal followed by T-bar removal tended to approach the bolts before the T-bars), but there was no reliable evidence that the chimpanzees preferentially used the observed actions to remove the objects.

The first of these findings, that the chimpanzees tended to approach the objects in the observed order, is interesting because it suggests that these apes have the first of the two necessary conditions for imitation specified by ASL theory (i.e., that they can learn a stimulus sequence by observation). On the other hand, the second finding is disappointing because it means that the artificial fruit studies have not (yet) provided compelling evidence of response learning by observation. If it had been possible to test a larger sample of chimpanzees, a significant tendency to use the same action as the demonstrator may have emerged. However, as Whiten and colleagues acknowledge, such an effect, whether it was found in capuchins (Custance *et al.*, 1999) or chimpanzees, could be due to emulation learning (Tomasello *et al.*, 1993b) rather than response learning by observation. In other words, the observers may be learning by observation the affordances or dynamic properties of the objects manipulated rather than the action applied. This is a possibility in the case of the artificial fruit procedure because, in the studies to date, object movement has been confounded with demonstrator movement. For example, when a bolt was twisted out, it rotated in one direction, and when it was poked out, it translated in the opposite direction (relative to compass points, the box, and the observer).

Three other ape studies have reported failure to find evidence of imitation using two-action tests. Tomasello, Call, and colleagues found that, in contrast with 2-year-old children, juvenile and adult chimpanzees (Nagell *et al.*, 1993) and orangutans (*Pongo pygmaeus*) (Call and Tomasello, 1994) showed no tendency to copy the action used by a human demonstrator to rake in food. Similarly, there were no signs of imitation when juvenile and adult orangutans observed a stick, which was protruding from a box, being manipulated in one of four ways by a human demonstrator (Call and Tomasello, 1995; Tomasello, 1996). (Procedures in which different groups of subjects are exposed to two or more distinct actions and assessed in terms of their subsequent performance of these actions are conventionally

known as two-action tests, regardless of the number of levels of the independent variable.)

Finally, two primate studies using procedures similar to those of the two-action method are worthy of consideration. In the first of these, Bugnyar and Huber (1997) gave marmosets (*Callithrix jacchus*) a test in which they could obtain food by pulling a door (hinged at the top) toward their bodies or by pushing it away. Prior to this test, one group of subjects observed a demonstrator pulling the door, whereas the other group had no previous exposure to the apparatus. Careful analysis of the test data revealed suggestive, but not conclusive, evidence that some marmosets in the observer group were influenced by the action they observed. However, in comparison with the nonexposed animals, the observer group did not show a reliable bias in favor of pulling the door.

In the second study, Myowa (1996) tested a single, infant chimpanzee (5–15 weeks of age) for imitation of human facial gestures in a procedure modeled on that of Meltzoff and Moore (1977). In weekly testing sessions, the chimpanzee was exposed to 15-s periods in which an adult human demonstrated tongue protrusion, lip protrusion, and mouth opening. These observation phases alternated with 20-s test periods in which the model adopted a passive face, and the facial gestures of the chimpanzee were recorded. Myowa reported that, for each of the three facial gestures, the chimpanzee was more likely to exhibit the recently observed gesture than the other two during test periods in Weeks 5–10.

These results are difficult to interpret because Myowa's (1996) study involved a single subject and the reliability of similar effects in human neonates has been questioned. In an extensive review and reanalysis of data on human neonatal imitation, Anisfeld (1991) found reliable evidence of demonstrator-consistent responding only in the case of tongue protrusion and pointed out that this effect could be due not to imitation but to a rebound effect. This hypothesis suggests that the baseline rate of tongue protrusion is depressed during observation periods by attention to the demonstrator and, in a compensatory fashion, increases above baseline in the subsequent test periods. However, even if observation of tongue protrusion causes tongue protrusion in neonates, in this isolated case the link between observation and execution could be innate.

Taken at face value, Myowa's (1996) findings could not be due to rebound effects because during the test periods there was a selective increase in the frequency of the previously demonstrated response. Furthermore, since this selective increase in frequency occurred for each of three actions, it is implausible, although not impossible, that the results were due to the operation innate stimulus-response links. Thus, Myowa's study is very interesting,

but it needs to be convincingly replicated before it can support any firm conclusions about imitation in primates.

The absence of clear evidence that primates are capable of response learning by observation does not, of course, imply that they are unable to do so. Indeed, it is more likely to reflect their inaccessibility relative to many rodents and birds. The costs of primate research often prohibit careful experimental investigation with large samples, and it is seldom possible to repeat a procedure several times with different groups of subjects of the same taxa and thereby to establish effective parameters and incorporate additional controls. For the same reasons, and because it is almost as difficult to monitor and control the preexperimental experience of nonhuman primates as it is for humans, a primate paradigm is unlikely to provide a suitable basis for analytic experiments (i.e., for research on the psychological mechanisms of imitation in general and investigation of the role of combinatorial novelty in particular).

B. RODENTS

In the first two-action test involving rodents, Collins (1988) allowed male mice (*Mus musculus*) to observe a female conspecific demonstrator from behind as the latter moved a pendulum door to the left or to the right for food reward. When subsequently given access to the door and rewarded for pushing it in either direction, the observer mice showed a reliable bias in favor of pushing the door in the same direction as did their demonstrator. This demonstrator-consistent response bias could have been due to response learning by observation, but it could also be that the mice learned about the action of the door rather than of the animal operating on the door. Substantiating this stimulus learning interpretation, Denny *et al.* (1983, 1988) reported that rats (*Rattus norvegicus*) exposed to a pendulum bar that moved, in the absence of a demonstrator, to the right for food and the left for no food or vice versa subsequently tended to push the bar in the direction that had been followed by reward.

Bidirectional control experiments, inspired by Grindley (1932) and conducted by our own group, seemed until recently to control for stimulus learning by observation and thereby to provide stronger evidence of imitation in rats (Heyes and Dawson, 1990; Heyes *et al.*, 1992, 1993, 1994; see Heyes, 1996, for a review). In the basic bidirectional control procedure, the observer confronted the demonstrator as the latter pushed a rigid pendulum or joystick to the "left" or to the "right" for food reward and was subsequently given access to the joystick from the position previously occupied by the demonstrator (Fig. 3). On test, the observers tended to push the joystick in the same direction relative to the actor's body as had
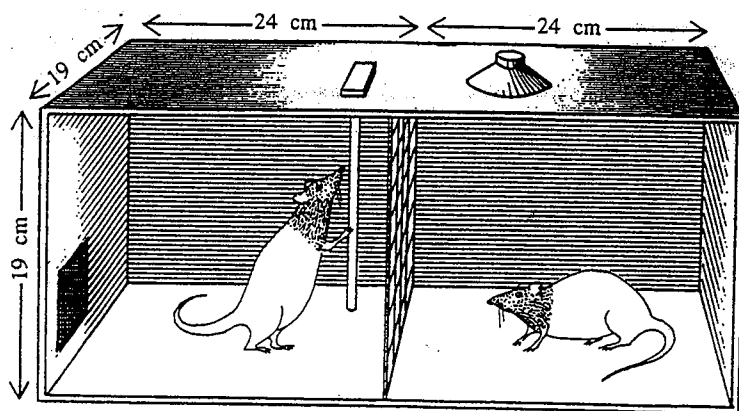
FIG. 3. Diagram of the apparatus used in bidirectional control tests for imitation in rats. Reprinted with the permission of the *Experimental Psychology Society* from Heyes and Dawson, 1990.

their demonstrators, despite the fact that this action resulted in the joystick moving in the opposite direction within the observer's visual field to that in which it had moved during observation (Heyes and Dawson, 1990). Furthermore, the effect persisted when the joystick was moved between observation and testing such that, on test, it moved in a plane perpendicular to that in which it had moved when acted on by the demonstrator (Heyes *et al.*, 1992). In these circumstances, when the observers moved the joystick in the same direction as the demonstrator, relative to the actor's body, it moved to a different location in space to that in which it had moved during conspecific observation.

However, the results of recent experiments (Mitchell *et al.*, 1998; Gardner, 1997) indicate that scent cues may influence rats' performance in the bidirectional control procedure and thereby cast doubt on this evidence of imitation. Mitchell *et al.* (1998) found that when the joystick is rotated 180° within its mounting between observation and test, observers show reliable demonstrator-inconsistent responding (i.e., a systematic tendency to respond in the opposite direction to their demonstrators). A plausible explanation for this is that the demonstrators deposit attractive odor cues on the side of the joystick contralateral to its direction of motion, and that exploration of these cues by the observers promotes a demonstrator-consistent response bias when the joystick remains in the same position on test and a demonstrator-inconsistent bias when it is rotated 180°.

An odor hypothesis of this kind, even one which assumes that demonstrators can deposit aversive and attractive scent cues on the joystick, does not explain all the published results of the bidirectional control procedure (Mitchell *et al.*, 1998). However, unless or until the basic effect is demonstrated with appropriate controls for scent cues (which may involve joystick cleaning or "box swapping"; Heyes *et al.*, 1998), the bidirectional control experiments cannot be regarded as providing sound evidence of response learning by observation in rats.

As a result, and given the ambiguity of the findings of Collins (1988) and Denny *et al.* (1983), the rodent literature does not currently include a paradigm with high potential for analytic investigation of the mechanisms of imitation.

C. BIRDS

The most promising evidence of imitation in animals presently comes from studies of birds, in particular, budgerigars, grackles, starlings, pigeons, and quail. We outline each of these studies and then consider them as a group in terms of whether they demonstrate response learning by observation of a combinatorially novel action or involve the use of a potentially accessible and reliable paradigm.

Dawson and Foss (1965) initiated, and Galef *et al.* (1986) developed, the use of the two-action method in their studies of budgerigars (*Melopsittacus undulatus*). In the experiment by Galef *et al.*, budgerigars that had observed a conspecific demonstrator removing the cover from a food dish using its beak or its feet showed a significant bias in favor of using the same appendage (beak or feet) as had their demonstrators. This effect was detected when performance on the first two test trials was combined but not on subsequent test trials. It is unlikely to have resulted from the D attracting the O's attention to a particular part of the apparatus because the published report suggests that the beak-using and feet-using demonstrators made contact with the same part of the cover. Furthermore, since birds are relatively insensitive to olfactory cues, and the observers and demonstrators worked on physically distinct pieces of apparatus, it is very unlikely that the observers' behavior was influenced by scent cues on the manipulandum. In principle, the subjects may have learned by observation about the trajectory of the cover (emulation learning) rather than about the actor's body movement (imitation). This possibility arises because the apparatus used for demonstrations was such that foot operations tended to tip the cover off the food cup, whereas beak operations tended to result in the cover sliding out of position. It is difficult to evaluate because there is no record of whether, on test trials, the observers used their beaks to slide the cover

and their feet to tip it off the food cup. However, it is unlikely that learning about the dynamic properties of the cover was solely responsible for demonstrator-consistent appendage use because the apparatus used on test trials allowed both trajectories to be achieved using both appendages.

Like budgerigars, Carib grackles (*Quiscalus lugubris*) and European starlings (*Sturnus vulgaris*) have provided evidence of imitation which is strong relative to that obtained from nonavian species but which could, in principle, have been influenced by emulation learning. Lefebvre *et al.* (1997) allowed grackles to observe one of two techniques being used to remove a stopper from an inverted tube containing food. One technique, which was demonstrated by conspecifics, involved open-beak probing and pulling movements, whereas the other demonstrated by Zenaida doves (*Zenaida aurita*) consisted of closed-beak pecking. On first contact with the tube apparatus, more of the observers of the closed-beak demonstration removed the stopper with a closed beak than with an open beak, and observers in this group made more closed-beak pecks than observers of the open-beak demonstration.

The starling experiment (Campbell *et al.*, 1998) employed a "two-object/two-action" test (Ray 1997). Observer birds were exposed to a conspecific demonstrator removing one of two stoppers (red or black) from a box containing food either by pulling the stopper up with a closed beak or by pushing it down into the box with an open beak. Thus, there were four groups of observers: red-up, red-down, black-up, and black-down. To remove the stopper for the first time, and in the course of three subsequent test trials, observers showed reliable tendencies both to remove the same stopper as their demonstrator removed and to do so using the same up/closed-beak or down/open-beak action.

A final group of bird studies, involving pigeons (*Columba livia*) and Japanese quail (*Coturnix japonica*), excluded the possibility of emulation learning (Zentall *et al.*, 1996; Kaiser *et al.*, 1997; Akins and Zentall, 1996, 1999). In these experiments, observers were exposed to a conspecific demonstrator pressing a treadle with its beak (group Pecking) or with its feet (group Stepping) 50 times for food reward. The treadle, which was mounted on an operant panel, moved through the same trajectory regardless of whether the action effecting treadle depression was pecking or stepping. Immediately after the demonstration session, observers were given access to the treadle, allowed to press it at least 50 times, and rewarded for each response regardless of whether it consisted of stepping or pecking. In these circumstances, both pigeons (Zentall *et al.*, 1996) and quail (Akins and Zentall, 1996) tended to use the same action as their demonstrators. Among the pigeons, 5 of 10 birds in group Pecking made pecking responses and 5 made stepping responses, whereas none of the 10 birds in group Stepping pecked the lever. In the case of the quail, the frequency of pecking was

significantly greater than the frequency of stepping in group Pecking, whereas the frequencies of stepping and pecking did not differ in group Stepping.

In comparison with previous studies, all these bird experiments provide strong prima facie evidence of imitation. That is, their results suggest that exposure to a demonstrator's behavior (and not to the object of that behavior) increased the probability that the observer would produce the same behavior (and not that it would simply be more active or direct its behavior to particular objects). The budgerigar, grackle, and starling studies did not completely exclude the possibility of emulation learning, and it would certainly be desirable for future experiments to do so. However, we consider the avian data to be strong for two reasons. First, there is no independent evidence that birds (or members of any other nonhuman species) are capable of the necessary kind of emulation learning (i.e., of learning to discriminate complex, dynamic properties of objects under conditions comparable to those of the budgerigar, grackle, and starling experiments). Second, the evidence that pigeons and quail show demonstrator-consistent responding in the absence of the opportunity for emulation learning supports the hypothesis that this kind of learning is not solely responsible for the effects reported in the other avian species.

The avian data are certainly strong enough to make it worthwhile to consider whether the target actions were combinatorially novel. Any post hoc assessment of combinatorial novelty is bound to be speculative, and our speculation is that it was low in these studies—that many of the components of the imitated actions had been contiguously observed and executed by the subjects prior to the experiments. In all cases, the observers had lived in the laboratory, in groups, or with visual access to other birds prior to the experiments. In these circumstances it is likely that they consumed the same foodstuffs at the same time as other birds and therefore that, through synchronous action, they had the opportunity simultaneously to observe and execute various foraging behaviors.

It might be objected that at least one of the avian imitation effects, treadle stepping in pigeons and quail, is unlikely to have arisen from previous experience of seeing and doing the target response because stepping is a relatively arbitrary foraging behavior. However, this is not a compelling argument for imitation of combinatorially novel actions for two reasons: (i) The evidence that observation of stepping promotes stepping in pigeons and quail is not conclusive and, even if it were, (ii) if birds have a tendency to peck when they see other birds peck, whether based on an innate link or correlated experience of seeing and doing, this would increase the likelihood that they have correlated experience of observation and execution of other lower frequency foraging behaviors, including stepping.

Perhaps the clearest point to emerge from our speculation about combinatorial novelty is that the only truly effective way of assessing its role in imitation is through experiments explicitly designed to do so, and in particular by varying pretest experience of seeing-and-doing components of the target action (see Section V). In our view, avian two-action tests have significant potential to provide a basis for analytic experiments of this kind. Budgerigars, starlings, pigeons, and quail (although not grackles) are all relatively easy to acquire and maintain as laboratory animals, and therefore it is possible to test a good-sized sample in each experiment and to repeat experiments (in the same and different laboratories) to adjust parameters and check the reliability of findings.

Research to date suggests that, of the studies involving accessible species, the two-object/two-action test with starlings and the treadle test with quail are likely to yield the most reliable effects. In their budgerigar study, Galef *et al.* (1986) reported a transitory effect, confined to the first couple of test responses, and noted that they had been unable to find a stronger or more durable effect in the course of 2 years of parameter variation. Similarly, Akins and Zentall (1996) switched from pigeons to quail because they found that a substantial proportion of observer pigeons either failed to respond on test or exhibited demonstrator-inconsistent behavior. In contrast, the effects found in starlings and quail have persisted throughout the test session, and each test has been replicated (A. Goldsmith *et al.*, unpublished results; Akins and Zentall, 1999).

The strength of the treadle test is that it controls for emulation learning, whereas the advantage of the two-object/two-action test is that it allows simultaneous investigation of stimulus learning and response learning by observation and thereby provides a method of comparing the conditions favoring nonimitative and imitative social learning (Ray, 1997). The treadle test could be adapted to the same purpose simply by adding a second treadle to the apparatus and allowing quail to observe pecking or stepping of the left or the right treadle. In a complementary way, a "ghost control" condition or transfer test could be added to the two-object/two-action test to examine the role of emulation learning (Heyes *et al.*, 1992, 1994). Ghost control starlings might be exposed, in the presence of a feeding conspecific, to the stopper rising up out of the food box or moving down into the box automatically (e.g., through the operation of fine wires). In a transfer test, starlings that had observed up/open-beak or down/closed-beak demonstrations could be tested using a manipulandum that does not move in the vertical plane.

In conclusion, this brief review suggests that (i) recent use of two-action tests has brought a new vigor and incisiveness to research on imitation in animals, (ii) the current evidence is consistent with the hypothesis that

imitation depends on previous experience of contiguously seeing-and-doing components of the to-be-imitated action sequence, and (iii) several avian paradigms are likely to be sufficiently reliable and accessible to support analytic experiments investigating the mechanisms of imitation learning.

VII.   POSTSCRIPT: IMITATION AND CULTURE

It has often been argued that imitation in animals is important with respect to our understanding of both cognition and culture; that in addition to involving complex psychological mechanisms, imitation plays a key functional role in the transmission and accumulation of information across individuals and generations (Tomasello *et al.*, 1993a; Tomasello and Call, 1997; Tomasello, 1999; Boyd and Richerson, 1985; Richerson and Boyd, 1999). In this article, we focus on the cognitive significance of imitation, but this is not to deny that there is any kind of special relationship between imitation and culture.

The most thorough contemporary analyses of the link between imitation and culture state or imply that (i) the psychological mechanisms of imitation are distinct from those of other forms of social and individual learning, in terms of both their "rules of operation" (Sherry and Schacter, 1987) and their evolutionary origins, and (ii) these mechanisms mediate information transmission with sufficient fidelity to support cultural evolution, a process analogous to natural selection which promotes behavioral adaptation. In contrast with the first of these hypotheses, ASL theory suggests that associative mechanisms of common phylogenetic origin underlie individual learning, nonimitative social learning, and imitation [see Lefebvre (1999) for data consistent with this hypothesis]. However, ASL theory also suggests that the capacity to imitate represents ontogenetic specialization of these general processes; that when, in the course of ontogeny, inputs to the general processes include contiguous observation and execution of action units (and/or acquired equivalence training), they yield an "imitation repertoire"—a set of action units that can be imitated when observed in novel sequences. ASL theory therefore implies that, to the extent that experience of seeing-and-doing action units derives from exposure to mirrors and to imitation of the observer's behavior by others, culture supports imitation (Heyes, 2000).

Of course, in addition to being supported by culture, imitation may play a special role in promoting cultural evolution. However, as argued by Heyes (1993), and in contrast with the second implication discussed previously, it would seem that fidelity of information transmission requires processes supporting faithful acquisition of information by one individual, *O*, from

another, *D, and* faithful retention processes ensuring that *O* does not lose or change the information before it is retransmitted to a third party. For the information contained in certain kinds of behavior, imitation may be an unusually effective acquisition process (compared with nonimitative social learning or language), but additional psychological processes promoting conformity to group norms (Wilson, 2000) are likely to be necessary to achieve the transmission fidelity required for cultural evolution.

VIII.   SUMMARY

Actions vary on the dimension of perceptual opacity. Highly perceptually opaque actions, such as facial expressions, give rise to dissimilar sensory inputs when observed and executed, whereas highly perceptually transparent actions, such as vocalizations and distal appendage movements, yield similar sensory inputs when observed and executed. The most significant challenge for any theory of the psychological mechanisms of imitation learning is to explain imitation of perceptually opaque actions. The theories that have addressed this problem in the past century are of two kinds: Transformational theories suggest that most of the information necessary to achieve a behavioral match is generated internally by complex cognitive processes, whereas associative theories claim that this information is derived principally from experience. These theories delineate plausible alternative accounts of the psychological mechanisms of imitation, but they do not provide a satisfactory framework for empirical inquiry because each theory either does not make testable predictions or is inconsistent with what is already known about the conditions of imitation.

The ASL theory suggests that imitation is mediated by associative processes which form links between sensory representations of successive components in an observed action sequence (horizontal processes) and between sensory and motor representations of individual action components (vertical processes). It predicts that reproduction of a novel sequence of action units is possible to the extent that the subject (i) can learn a stimulus sequence by observation and (ii) has prior experience of contiguously observing and executing components of the novel sequence and/or acquired equivalence training for those components (i.e., when the sequence has low combinatorial novelty). The latter prediction can be tested more readily with animal than with human subjects, and a survey of research using two-action tests of imitation suggests that several paradigms involving avian subjects are sufficiently reliable and accessible to support analytic experiments of the relevant kind.

Thus, the principal significance of imitation in animals lies in its potential to provide insight into the psychological mechanisms of imitation learning, and recent methodological innovations have brought it to the brink of realizing this potential. The most pressing current requirement is to formulate both transformational and associative theories of imitation which make empirically testable predictions.

Acknowledgments

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